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Flow-related effects in prawn-trawl codends: potential for increasing the escape of unwanted fish through square-mesh panels

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Abstract.—Two experiments were done in a flume tank to quantify the effects of codend mesh circumference and weight of catch on water flow. The mesh circumference of the posterior section of prawn-trawl codends (with and without bycatch reducing square-mesh panels) were assessed with three weights of catch (30 kg, 50 kg, and 70 kg). Compared with a codend with a circumference of 100 meshes throughout its entire length, a codend with an anterior section of 100 meshes and a posterior section of 200 meshes in circumference significantly increased the displacement of water forwards (up to 1120 mm from the end of the codend). This result varied with the weight of catch in the codend. The second experiment involved placing composite panels of square-shaped mesh (bycatch reducing devices) into the tops of the anterior sections of two codends with the same configurations as those above (termed the "100 panel codend" and "200 panel codend," respectively). There was a displacement of water forwards immediately under the square-mesh panel in the 200 panel codend (by up to 2200 mm from the end of the codend). The results are discussed in terms of 1) the probable effects that codend mesh circumference and water displacement in codends have on fish behavior, and 2) implications for the future development of bycatch reducing devices like square-mesh panels in prawn-trawls.

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Oceanic prawn-trawling occurs from nine major ports in New South Wales (NSW) Australia and has a total value of approximately A$17 million per annum. The principal target species is the eastern king prawn (*Penaeus plebejus*), although a significant proportion of the total value is derived from the sale of legally retained bycatch comprising individuals of several species of fish, crustaceans, and cephalopods (see Kennelly, 1995). In addition to this landed catch, however, significant numbers of nontarget organisms of no commercial value are also captured and discarded, including juvenile fish of species which, when larger, are targeted in other commercial and recreational fisheries (Kennelly, 1995).

Concerns over the incidental capture and mortality of large numbers of juvenile fish have led to the development of various bycatch reducing devices (BRDs), designed to minimize undesirable bycatch while maintaining catches of prawns and other commercially valuable individuals (Broadhurst et al., 1996; Broadhurst and Kennelly, 1996; 1997). In particular, a new design comprising composite panels of square-shaped mesh (referred to as the composite square-mesh panel) was shown to increase catches of prawns (by up to 14%) (Broadhurst and Kennelly, 1997) while significantly reducing up to 40% of total unwanted bycatch and up to 70% of the numbers of small individuals of commercially important species such as whiting (*Sillago* spp.) (Broadhurst and Kennelly, 1996).

The results from these experiments are attributed primarily to differences in the behavior of fish and prawns in the trawl. Fish are believed to be herded close together in the anterior section of the codend, upsetting the normal balance of the school and initiating an escape response towards the sides and top of the net and out through the open square-shaped meshes (Broadhurst and Kennelly, 1996). A contributing factor towards this escape is the displacement and change in direction of water flow due to the circumfer-

ence of meshes in the posterior section of the codend. In an experiment to test this hypothesis, Broadhurst and Kennelly (1996) showed that a conventional codend made from an anterior section of 100 meshes circumference and a posterior section 200 meshes in circumference (a common commercial configuration) was less selective (i.e. retained more bycatch) than a conventional codend with a 100 mesh circumference throughout its entire length (see also Robertson and Stewart, 1988; Armstrong et al., 1990; Reeves et al., 1992; Galbraith et al., 1994). However, a comparison of codends with the same netting configurations as above but containing composite square-mesh panels located in their anterior sections showed that the effects on selectivity due to increased circumference in the posterior section were negated by a significant increase in the escape of small fish (e.g. red spot whiting, *Sillago flindersi*) through the square meshes.

These results led to the hypothesis that increased twine area and smaller mesh openings in codends with posterior sections of 200 meshes circumference increased the displacement of water forwards and out through the meshes in the anterior section (see also Watson, 1989). In turn, this water movement may have 1) physically directed small fish out through the strategically positioned composite square-mesh panel; 2) assisted them to maintain position in front of the catch in the codend, increasing their likelihood of randomly encountering square meshes; and (or) 3) stimulated their lateral line receptors and thus their overall escape response. The reaction of prawns to this stimuli was thought to be minimal, given their inability to sustain escape responses in trawls (see Lochhead, 1961; Newland and Chapman, 1989).

Although the results from the paper discussed above led to several hypotheses about changes in water flow and fish behavior due to changes in codend geometry, we lacked the quantitative information on flow rates necessary to support or refute them. Such information is important for developing new designs of codends and understanding where to position square-mesh panels and other BRDs. Our goals in the present study were to quantify the effects on water flow at various positions in codends and under square-mesh panels in two flume tank experiments. We simulated commercial conditions in the flume tank by using different weights of catch in various codend designs.

Materials and methods

Two experiments were undertaken in May 1996 at the Australian Maritime College with the Faculty of Fisheries and Marine Environment's flume tank. This facility consists of a recirculating flow tank of fresh water, measuring 17.2 m long, 5 m wide, and 2.5 m deep and comprises three levels: 1) an upper level where nets, etc., are placed into the tank; 2) an observation level, with a continuous perspex viewing-window; and 3) a water-return channel. The two lower levels feature a series of delivery bends and screens that maintain constant water velocity throughout the depth of the tank without any swirls or vortices. Several electric motors, hydraulic pumps, and impellor shafts provide water flow of up to 1.5 m/s.

An electromagnetic current meter was attached to the base of a stainless steel stanchion (Fig. 1A) and linked to a computer by means of a coaxial cable. The stanchion was attached to a movable carriage positioned on rails over the upper level of the flume tank. This assembly enabled the current meter to be repeatedly located at several predetermined positions within the tank.

A full-scale Florida flyer prawn-trawl (material: 18 ply twine; mesh size: 40 mm) with a headline length of 5.4 m, was rigged to two fixed stanchions, located on the sides of the forward section of the flume tank. The trawl was rigged with a zipper (no. 10 nylon open-ended auto-lock plastic slides) to facilitate changing the codends. The codends used in the experiments were of normal commercial size and materials, measuring 58 meshes long (2.3 m) and constructed from 40-mm mesh netting and 60-ply UV-stabilized high-density polyethylene twine. These codends comprised two sections: the anterior section, which was 33 meshes long and attached to a zipper and the posterior section, which was 25 meshes long (for details see Fig. 1, B and C —see also Broadhurst and Kennelly, 1996).

Experiment 1

Two codend designs were compared. The codends (termed the 100 and 200 commercial codends) were made entirely of diamond-shaped meshes and comprised anterior sections with a circumference of 100 meshes, attached to posterior sections with circumferences of 100 and 200 meshes, respectively (Fig. 1, B and C). Three incisions of the same size as the width of the current meter's stanchion (three meshes in length), were made in the tops of each codend at distances of 2200 mm, 1120 mm, and 560 mm forward from the end of the codends to facilitate placement of the current meter inside the codends (Fig. 1B).

Experiment 2

The two codends compared in this experiment were similar to the 100 and 200 commercial codends de-

scribed above but included composite square-mesh panels made of 60-mm and 40-mm netting (3-ply and 48-ply UV-stabilized high-density polyethylene twine, respectively) cut on the bar and inserted into the tops of the anterior sections (termed the 100 panel and 200 panel codends) (for details see Fig. 1C and Broadhurst and Kennelly, 1996). Because the current meter (and not its stanchion) was inserted only 5 cm into the tops of the codends (Fig. 1C), it was not necessary to cut the meshes of these codends. Instead, four positions were labeled with a permanent marker at 2200 mm, 1720 mm, 1490 mm, and 1130 mm forward from the end of the codends (Fig. 1C).

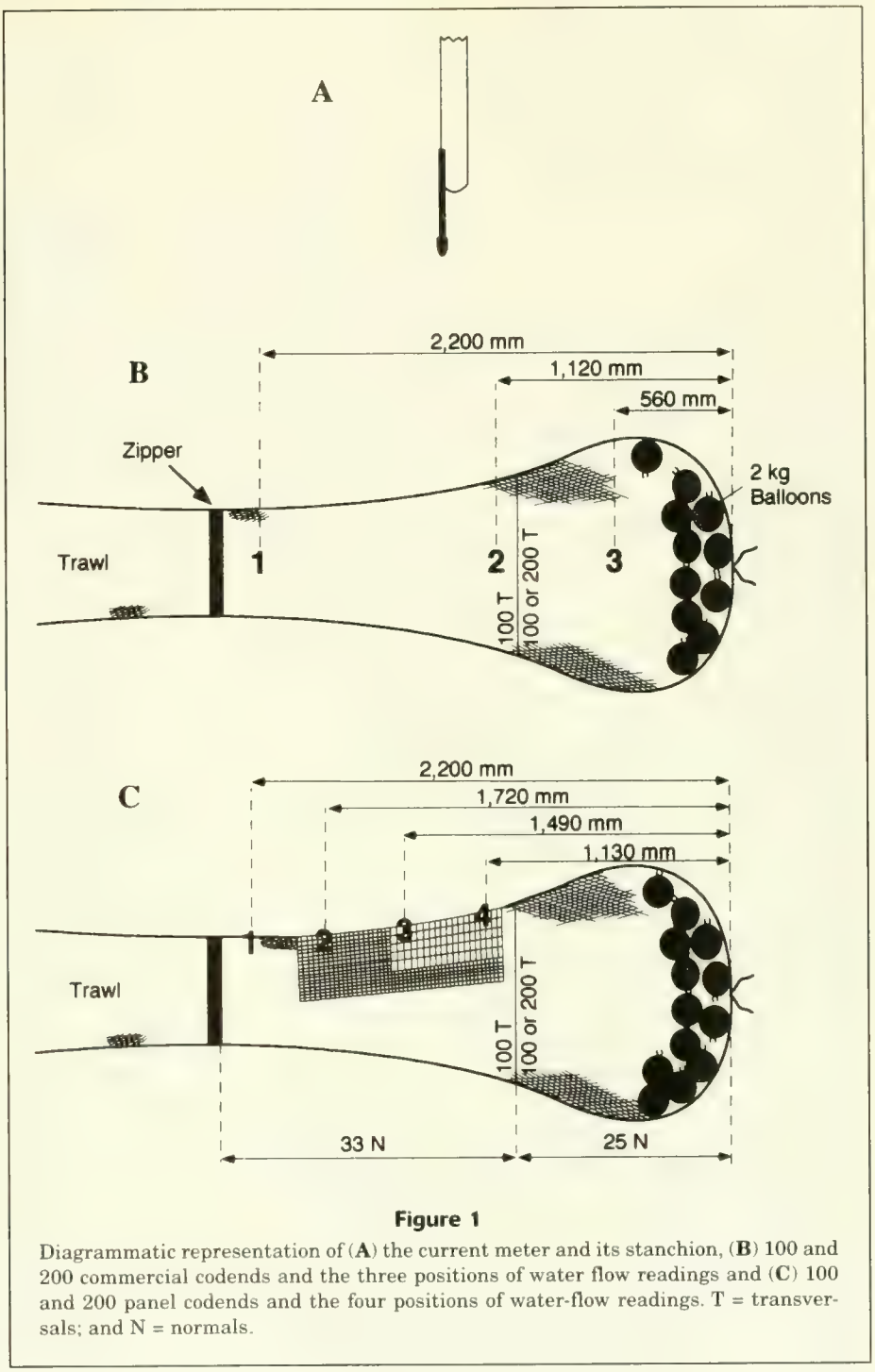

Figure 1

Diagrammatic representation of (**A**) the current meter and its stanchion, (**B**) 100 and 200 commercial codends and the three positions of water flow readings and (**C**) 100 and 200 panel codends and the four positions of water-flow readings. T = transversals; and N = normals.

Experimental procedure

Thirty five rubber balloons were each filled with 2 liters of water, providing a total mass (in air) of 70 kg. These balloons were used to simulate masses of catch in the codends. In each experiment, the two codends were tested alternately. The particular codend to be examined was attached to the trawl and loaded initially with 15 balloons (i.e. 30 kg). The hydraulic pumps in the flume tank were activated and adjusted to produce a flow of 1.2 m/s (the standard towing speed during commercial operations). After a stabilizing period of 10 minutes, the stanchion containing the current meter was alternately lowered into each of the predetermined positions in the codends (three in experiment 1 and four in experiment 2). After a further stabilizing period of one minute at each position, the current meter was switched on and left for a period of one minute, during which the flow of water immediately anterior to the current meter was recorded at one second intervals and the data were transmitted to the computer. The mean flow rate from each minute of recording was calculated from these data and used in subsequent analyses. After each reading, the current meter was moved to the next position and the procedure repeated. After six replicate readings were collected for each position, the flow of water in the flume tank was reduced to approx. 0.5 m/s and additional balloons were added to the trawl to simulate an increase

in the volume of catch. The above procedure was then repeated to obtain data on the flow of water at each position with 50 kg (25 balloons) and 70 kg (35 balloons) in each codend.

Data analysis

Data collected in each experiment were examined by using Cochran's test for homogeneity of variances and transformed if necessary. Data from experiment 1 were analyzed in a three-factor fully orthogonal, balanced analysis of variance. The factors were codends, positions, and weights. Data from experiment 2 were analyzed at each position in two-factor fully orthogonal, balanced analyses of variance (Underwood, 1981). Significant differences detected in these analyses were investigated by Student-Newman-Keuls (SNK) multiple comparisons of means.

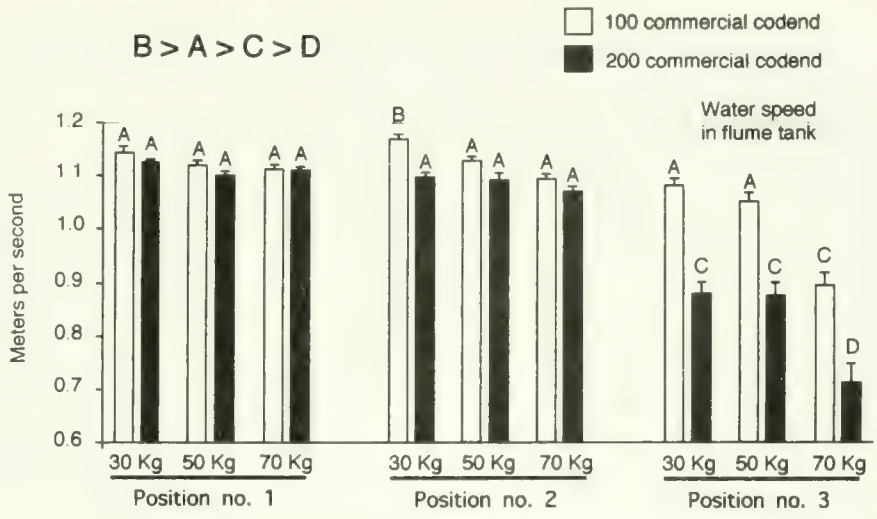

Figure 2

Differences in mean flow rates ±SE between the 100 and 200 commercial codends tested in experiment 1 (< and > indicate direction of differences in SNK tests).

Results

Experiment 1

The analysis of variance showed that there were significant differences in flow rates between the type of codend, position of the current meter and weight in the codend, and significant interactions among codend-type, positions and weights (Table 1). SNK tests showed that mean water flow was greatest at position no. 2 (1.162 m/s) in the 100 commercial codend with a catch of 30 kg and lowest at position no. 3 (0.709 m/s) in the 200 commercial codend with 70 kg (Fig. 2). SNK tests also showed that, compared with the 100 commercial codend, there was a significant reduction in mean water flow in the 200 commercial codend with 30 kg at position no. 2 (mean difference of 0.071 m/s) and across all three weights (30 kg, 50 kg, and 70 kg) at position no. 3 (mean differences of 0.203 m/s, 0.176 m/s and 0.184 m/s, respectively) (Fig. 2; Table 1). Although SNK tests did not detect differences in mean water flow between codends with 50 kg and 70 kg at position no. 2, nor across all weights at position no. 1, these combinations of weight and position showed trends similar to those described above—i.e. a mean reduction in water flow with the 200 commercial codend (Fig. 2).

Table 1

Summaries of F ratios from the analysis of variance to determine effects on water flow due to different codends (i.e. 100 and 200 commercial codends), position of current meter and weight in the codend. The square-root (sqrt(×)) transform was used to stabilize variances. In all tables $^{*}P = <0.05$; $^{**}P = <0.01$.

Treatment	df	Water flow (m/s)
Codends (C)	1	162.52**
Position (P)	2	388.16**
Weight (W)	2	62.42**
C × P	2	35.01**
C × W	2	8.04**
P × W	4	12.39**
C × P × W	4	0.81
Residual	90	

Experiment 2

There were significant differences in the mean water flow between the type of codend at position nos. 2, 3. and 4 and between weights at position nos. 2 and 3 (Table 2). There was a significant interaction between the type of codend and weight at position no. 1. SNK tests detected differences in the mean flow rates between the 100 and 200 panel codends at

Table 2

Summaries of F ratios from analyses of variance to determine effects on water flow at different positions due to different codends (i.e. 100 panel vs. 200 panel) and weights. The transforms used to stabilize variances (if required) are also listed.

Treatment	df	Position no. 1	Position no. 2	Position no. 3 sqrt(×)	Position no. 4
Codend (C)	1	2.21	5.88*	5.16*	7.92**
Weight (W)	2	2.29	3.95*	8.56**	1.34
C × W	2	7.81**	0.87	0.74	2.77
Residual	30				

position nos. 1, 3, and 4 (Fig. 3). Compared with the 100 panel codend, there was significantly less water flow in the 200 panel codend with a catch of 70 kg at position no. 1 (0.115 m/s difference between means) and at position no. 3 with 50 kg (difference of 0.102 m/s) (Fig. 3, A and C; Table 2). Conversely, at position no. 4, SNK tests detected an increase in the mean water flow in the 200 panel codend with a catch of 30 kg, compared with the 100 panel codend (difference of 0.067 m/s) (Fig. 3D). There was also a similar, although not significant result for 50 kg at this position. There were no other significant differences, although, at position nos. 2 and 3, there were similar trends across all weights (i.e. a reduction in water flow in the 200 panel codend) (Fig. 3, B and C).

Discussion

This study showed that the weight of catches and the configuration of the posterior section in codends can have significant effects on the displacement of water in the anterior section of codends. In interpreting these results, it is important to note that under the simulated conditions in the present study, water was forced through a stationary trawl (at 1.2 m/s). Any localized displacements of water forwards in the codends examined in this study, therefore, can be expressed as a reduction in the flow entering the trawl and calculated by subtraction from 1.2 m/s.

The flow of water at all positions in the four codends tested was less than 1.2 m/s, indicating that there was displacement of water anterior to the catch. However, the degree of this anterior water displacement varied significantly between the codends tested in each experiment (Figs. 2 and 3). For example, in experiment 1, the 200 commercial codend showed a significant increase (compared to the 100 commercial codend) in the displacement of water forwards at position no. 3 across all weights of catch (difference in mean flow of up to 0.203 m/s [Fig. 2; Table 1]). These differences in flow may be attributed primarily to the distribution of the balloons used to simulate catch in the two codends and consequent changes in codend geometry. In the 200 commercial codend, the balloons were observed to spread out evenly in the posterior section, providing a greater surface area of catch incidental to the flow than in the 100 commercial codend. This effect, combined with the increase in the area of twine in the 200 commercial codend probably caused an increase in the displacement of water forwards in this codend.

The above effects in the 200 commercial codend were also detected at position no. 2 with 30 kg of balloons and, although ANOVA failed to detect significant differences for the other weights at this position, the trends in the results were similar (i.e. a reduction in flow in the 200 commercial codend compared with the 100 commercial codend [Fig. 2; Table 1]). At position no. 1, for all weights, the force of the displaced water in front of the 200 commercial codend had dissipated to the extent where there were no significant differences between the two codends (Fig. 2; Table 1). It can be assumed, therefore, that the major influence of increased codend circumference on water displacement in the middle of the 200 commercial codend probably occurred up to some point between position nos. 2 and 3 (560 mm to 1120 mm from the end of the codend), in relation to the weight of catch.

In experiment 2, the effects of increased codend circumference on water displacement under the square-mesh panel were detectable at a greater distance from the end of the codend than those described above. Compared with the 100 panel codend, there were significant reductions in flow (corresponding to an increased displacement of water forwards) in the 200 panel codend at position nos. 1 and 3 (2200 mm and 1490 mm from end of the codend) with a weight of catch of 70 kg and 50 kg, respectively (mean differences in flow of 0.115 m/s and 0.102 m/s, respectively) (Fig. 3, A and C; Table 2). Although not significant, there were similar trends at position no. 2 for each weight and at position no. 3 for 30 kg and 70 kg (Fig. 3, B and C; Table 2). In contrast, there was a

significant increase in the flow of water at position no. 4 in the 200 panel codend with 30 kg and a similar result (though not statistically significant) for 50 kg (Fig. 3D; Table 2). This anomaly may be explained by the fact that the balloons in the 200 panel codend (like those in the 200 commercial codend) were orientated evenly across the surface area of the posterior section, increasing its diameter and decreasing the angle of incidence of its netting as it led into the anterior section of the codend at position no. 4. Although the current meter was located immediately under the composite square-mesh panel, at this position it was effectively aligned slightly above the anterior section of the codend and may have been influenced by the current outside the trawl, negating some of the flow-related effects of codend mesh circumference.

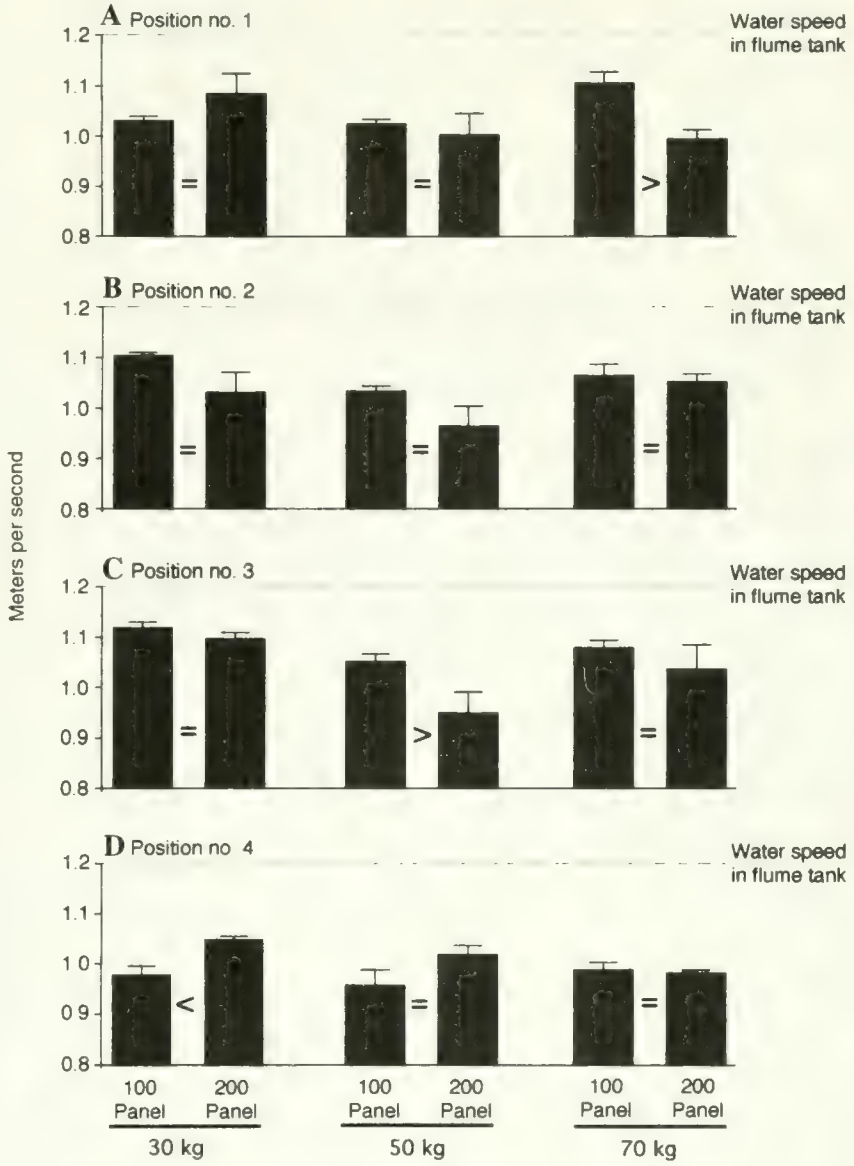

Figure 3

Differences in mean flow rates ±SE between the 100 and 200 panel codends tested in experiment 2 for each position of the current meter and for different weights (< and > indicate direction of differences in SNK tests of means).

With the exception of this latter result, the measured reductions in flow at most positions in the 200 codends (corresponding to increases in water displacement forwards) support the hypothesis that an increase in the circumference of meshes in the codend contributes towards the escape of small fish (between 5 and 20 cm) through the composite square-mesh panel (see Broadhurst and Kennelly, 1996; 1997). The size of these fish suggests that they are using anaerobic muscle power to maintain position in the moving trawl (1.2 m/s) and are fatigued when they enter the codend (see Beamish, 1978; Wardle, 1989). A relatively small increase in the displacement of water forwards (e.g. 0.203 m/s at position no. 3 in the 200 commercial codend or 0.1 m/s at position no. 3 in the 200 panel codend) may be sufficient 1) to assist small fish to swim forwards and out through the square meshes in the panel and [or] 2) to enable them to reduce their tail-beat frequencies and maintain their position in the codend for a longer period, increasing their chances of random escape through the panel; and [or] 3) to stimulate their lateral line receptors and thus their overall escape.

Without direct observations of fish swimming in the codend, it is difficult to determine their specific behavior during escape. Whatever their actual escape mechanism, however, the results obtained in this study provide important information for the subsequent design and location of BRDs like the com-

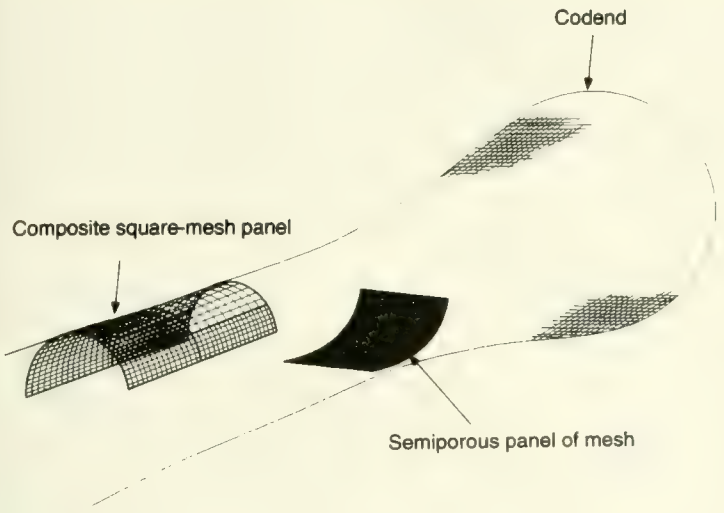

Figure 4

Diagrammatic representation of proposed modification to codends containing the composite square-mesh panel.

posite square-mesh panel. It is apparent that to maximize the effects of anteriorly displaced water in the posterior section of codends, the composite square-mesh panel should be located as close as possible to the end of the codend, but sufficiently in front of the anticipated build-up of catch to prevent prawns from accumulating past the square meshes and escaping through them. A solution to this problem would be to increase the codend mesh circumference in the posterior panel (i.e. the 200 panel codend), causing the catch to spread laterally in the back of the codend, rather than to accumulate in front. Although such a modification would also increase surface area, displacement of water forwards, and probably enhance fish escape through the square-mesh panel, it would also reduce mesh openings and the selectivity of the codend itself (Broadhurst and Kennelly, 1996).

An alternative modification that may increase displacement of water forwards (other than increasing codend circumference and catch) is to move the composite square-mesh panel forward in the codend and create areas of "artificial catch" by using semiporous panels (e.g. those with fine mesh). These could be positioned on the bottom of the codend, behind the panel and at an angle to the direction of tow (e.g. see Fig. 4). Such modifications would produce similar flow-related effects as those observed in our study, i.e. they would displace water anteriorly, directing fish towards the panel. Future research into the refinement of square-mesh panels and other BRDs in prawn-trawls that exploit the behavioral differences of fish in trawls, may benefit from these or similar modifications.

Acknowledgments

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An analysis of environmental effects on survey catches of squids *Loligo pealei* and *Illex illecebrosus* in the northwest Atlantic

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Abstract.—An analysis of environmental effects on autumn survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted. Research survey data collected during 1967–94 were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. We examined habitat associations of both species by using randomization methods and found that *L. pealei* was consistently associated with all of the environmental factors examined. In comparison with *L. pealei*, catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches, with the ratio of juvenile to adult catches decreasing with depth. Depth had a similar, but less pronounced, effect on *I. illecebrosus* catches. Time of day also affected *L. pealei* and *I. illecebrosus* catches. Catches of both species were lowest at night and diel effects were more pronounced for juveniles than for adults. Bottom and surface temperatures had a substantial effect on catches of juvenile and adult *L. pealei* but had a variable influence on *I. illecebrosus* catches. The joint effects of depth stratification, time of day, and annual squid abundance on survey catches were also analyzed to determine correction factors for diel differences in catchability of juvenile and adult squid. Significant diel differences in catchability were detected for juvenile and adult *L. pealei* and for juvenile *I. illecebrosus* and diel correction factors were determined for survey catches of these size categories. In contrast, significant diel differences in catchability of adult *I. illecebrosus* were not detected.

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An analysis of environmental effects on survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted for the continental shelf of the United States in the northwest Atlantic. Research survey data, collected during autumn, were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. Both squids grow rapidly (Brodziak and Macy, 1996; Dawe and Beck[1]), appear to live less than one year (Hurley et al., 1985; Macy, 1995; Brodziak and Macy, 1996; Dawe and Beck[1]), and undertake seasonal migrations in response to fluctuations in food availability, water temperature, and spawning (Lange and Sissenwine, 1983; Rowell et al., 1985a; O'Dor and Coelho, 1993). The rapid growth and short lifespan of these sympatric species suggest that environmental conditions were probably important determinants of their distribution and abundance on the continental shelf.

We investigated whether there was empirical evidence of habitat associations for both species by applying the habitat association method of Perry and Smith (1994). This randomization method accounted for the stratified random sampling design of the Northeast Fisheries Science Center (NEFSC) survey and tested whether catches within a year were associated with depth, time of day, surface temperature, and bottom temperature. Within-year associations that were consistent through time indicated which environmental conditions affected distribution and also provided a qualitative indication of habitat preferences.

We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Juveniles and adults of both species tend to differ in their food habits (Vovk, 1972; Vinogradov and Noskov, 1979; Macy, 1982; Maurer and Bowman, 1985) and, as a result, may use different habitats for feeding. We compared the effects of average depth of tow, time of day,

[1] Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES Council Meeting, Shellfish Committee/K, 33 p.

and surface and bottom temperature on survey catches to determine whether the habitat preferences of juveniles and adults overlap. Potential effects of different categories of depth, time of day, and surface temperature and bottom temperature on mean catch per tow were tested for juveniles and adults of both species, and the potential impacts on the ratio of juvenile to adult catches were also examined. These analyses also suggested whether environmental effects were similar for these sympatric species, because the degree of spatial overlap between their geographic distributions is at a maximum during autumn.

Last, we evaluated the relative magnitude of diel effects on juvenile and adult squid catches in relation to survey design and fluctuations in annual squid abundance. Previous bottom trawl studies have shown that diel effects on catches of *L. pealei* and *I. illecebrosus* can be important (Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Arkhipkin and Fedulov, 1986; Shepherd and Forrester[2]) because greater catchability occurs during the day. As a result of diel vertical migrations, night catches of these two species can be biased low in relation to day catches. To account for diel effects on minimum swept-area estimates of *L. pealei* biomass and stock size, diel correction factors have been used to adjust nighttime bottom trawl catches to daytime equivalents (Lange and Sissenwine, 1980, 1983). However, these correction factors were developed for total numbers of squid and were not size specific, even though Sissenwine and Bowman (1978) noted that a sixfold difference between the diel correction factor for weight and numbers of *L. pealei* suggested differential vertical migration by size. In this study, we applied a general linear model to determine size-specific diel correction factors for *L. pealei* and *I. illecebrosus* that accounted for potential effects of survey design and fluctuations in annual abundance. When diel effects were significant, correction factors were determined to standardize nighttime catches to daytime units.

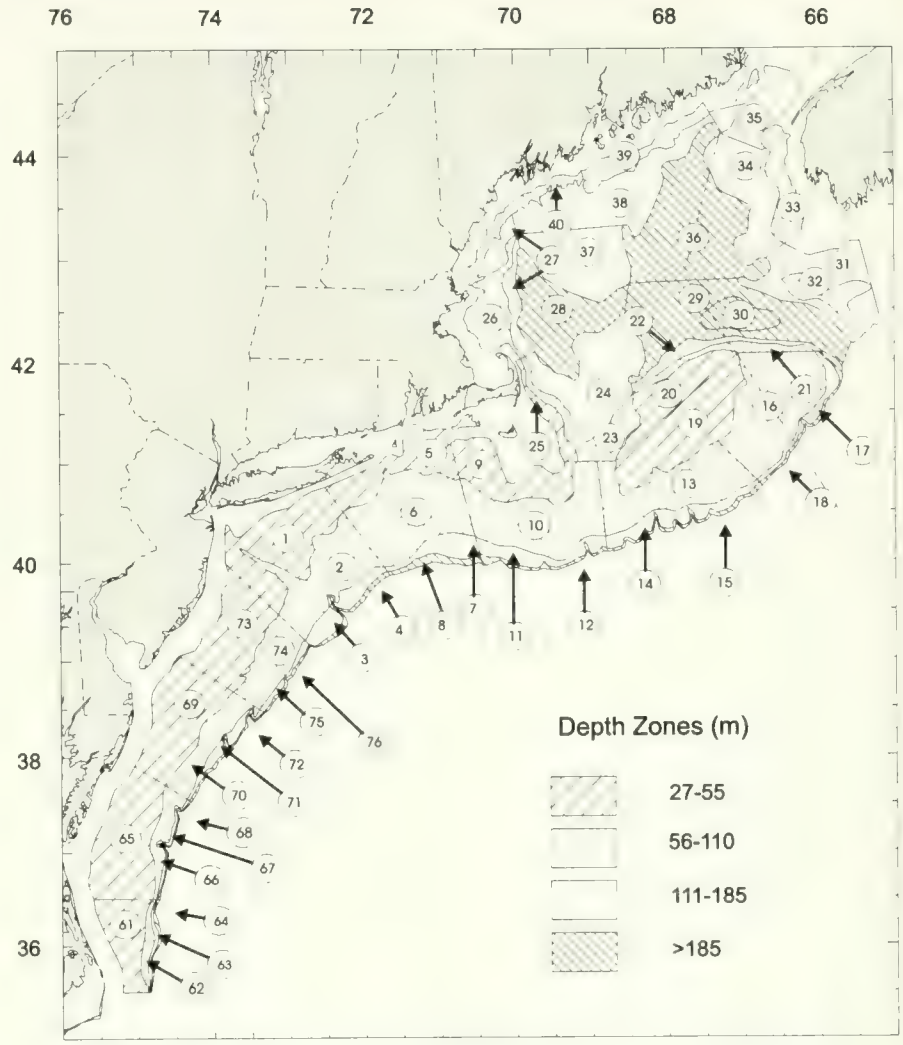

Figure 1

Offshore depth strata for autumn Northeast Fisheries Science Center bottom trawl surveys, 1963–94.

Materials and methods

Survey data

Research survey data were analyzed from NEFSC autumn bottom trawl surveys conducted during 1967–94 between Cape Hatteras, North Carolina, and the Gulf of Maine. In general, autumn surveys were conducted from mid-September through mid-

[2] Shepherd, G., and J. Forrester. 1987. Diurnal variation in catchability during bottom trawl surveys off the Northeastern United States. ICES Council Meeting 1987/B:44 (mimeo), 15 p.

October and along a similar cruise track each year. Standardized survey gear, procedures, and the stratified random sampling design are described in Azarovitz (1981). Offshore survey strata are defined by four depth zones; ranging between 27 m and 366 m. Strata numbers 1–30, 33–40, and 61–76 were included in our analyses (Fig. 1). Sampling was conducted 24 hours a day. Autumn survey data were used because only in autumn are both squid species distributed primarily within the survey sampling area. Survey data during 1963–66 could not be analyzed because catches of squid were not separated by species during these years.

At each randomly selected survey station, sampling was performed with a no. 36 Yankee otter trawl rigged with roller gear. Only standard tows, consisting of 20–30 minutes duration at a vessel speed of 3.5 knots, were included in the analyses. After each tow, the total weight of *L. pealei* and *I. illecebrosus* was measured to the nearest 0.1 kg, each species was enumerated, and length-frequency data (mantle length [ML] measured to the nearest cm) were collected. The following hydrographic and navigational data were recorded for each station: depth at the start and end of every tow (m), time of tow (h:m, Eastern Standard Time), bottom water temperature (°C), and surface water temperature (°C). Towing depth was computed as the average of depths recorded at the start and end of each tow. Surface water temperature was included in this analysis because the effect of surface temperature on the vertical distribution and catchability of these squids was unknown but was anecdotally important and potentially different from the effect of bottom temperature during autumn. In general, bottom and surface water temperatures within the survey region vary during autumn owing to the transition from a stratified water column, characteristic of summer, to a well-mixed condition typical of winter (Bowman, 1977). In particular, the relationship between surface and bottom water temperatures varied on an annual basis during the 1967–94 autumn surveys. Surface and bottom temperatures were not significantly correlated in 8 out of 28 years (29%), and exhibited a positive correlation ($\bar{\rho}$ =0.43) in 19 out of 28 years (68%) during 1967–94.

When an environmental factor was not measured at a survey station, that station was excluded from the association test for that factor. Stations with missing environmental measurements occurred at random, with the exception of the Georges Bank portion of the autumn 1990 survey when no bottom temperature measurements were made. In total, 7177, 7179, 6105, and 6280 stations were available for the association tests of squid catch with depth, time of day, bottom temperature, and surface temperature, respectively.

Within-year associations

Perry and Smith (1994) developed a nonparametric test of association between an environmental factor and the quantity of catch during a stratified random survey. Their method uses the maximum absolute difference between the cumulative distribution function (CDF) of an environmental factor and the catch-weighted CDF of that environmental factor as a test statistic in a randomization procedure to evaluate whether a significant association exists. In particular, the test algorithm is as follows. First, the empirical CDF (f) of the environmental factor is computed as

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{ih}), \tag{1}$$

where t = the value of the environmental factor;
h = an index for the survey strata;
i = an index for the tow in stratum h;
x_{ih} = the observed value of the environmental factor from the i^{th} tow in stratum h;
W_h = the proportion of the survey area in stratum h;
n_h = the number of tows in stratum h; and
$I(x)$= an indicator function with $I(x)$=1, when $x \le t$, and $I(x)$=0, when $x > t$.

Second, the empirical cumulative distribution of catch as a function of the environmental factor (g) is computed as

$$g(t) = \sum_h \sum_i \frac{W_h y_{ih}}{n_h \bar{y}_{st}} I(x_{ih}), \tag{2}$$

where $$\bar{y}_{st} = \sum_h W_h \bar{y}_h ,$$

and where y_{ih}= the catch from the i^{th} tow in stratum h;
$\bar{y}_h$ = the mean catch in stratum h; and
$\bar{y}_{st}$ = the stratified mean catch.

In Equation 2 above, the quotient $y_{ih}/\bar{y}_{st}$ expresses the relative catch under environmental condition x_{ih} in comparison with the stratified mean. The maximum absolute value of the difference between $f(t)$ and $g(t)$ over all values of the environmental factor is the observed test statistic (T) where

$$T = \underset{\forall t}{MAX} \left| \sum_h \sum_i \frac{W_h}{n_h} \left(\frac{y_{ih} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{ih}) \right|. \tag{3}$$

To evaluate whether the test statistic is significant, the observed environmental measurements (x_{ih}) are randomly sampled with replacement and assigned to observed catches with probability W_h/n_h under the hypothesis that the association between catch and the environmental factor is random. The value of the test statistic (T_R) is then computed for this random assignment. The randomization procedure of assigning environmental measurements to catches and of computing the value of T_R is repeated a large number of times to generate a distribution of test statistics for the null hypothesis of random association between catch and environmental factor. Last, the observed test statistic T is compared to the distribution of test statistics T_R from the randomization procedure to evaluate whether the null hypothesis of random association can be rejected.

We applied this test to *L. pealei* and *I. illecebrosus* catch, in numbers per tow, using four environmental factors: average depth of tow, time of tow, bottom water temperature, and surface water temperature. A total of 2000 randomizations were performed to provide an empirical distribution based on 2001 test statistics, including the original test statistic.

Size-specific environmental effects

Size-specific environmental effects on mean catches were evaluated separately for each species using tows that captured both juveniles and adults to ensure that comparisons were made under the same environmental conditions and that the ratio of juvenile to adult catch was well defined. Catch numbers of squid were separated into prerecruit (≤8 cm ML for *L. pealei* and ≤10 cm ML for *I. illecebrosus*) and recruit (>8 cm ML for *L. pealei* and >10 cm ML for *I. illecebrosus*) size categories, where prerecruits and recruits roughly corresponded to juvenile and adult squid. In what follows, prerecruit and recruit categories will sometimes be colloquially referred to as juveniles and adults, respectively. However, both *L. pealei* (Macy, 1980) and *I. illecebrosus* (Coelho and O'Dor, 1993) exhibit variability in sex-specific size at maturity, and for both species, an unmeasured fraction of smaller individuals within the recruit category were juveniles. The effect of depth on mean catch was evaluated first. Tow depth was categorized according to the depth zones used to define offshore strata of the NEFSC bottom trawl surveys: depth zone I (27–55 m), zone II (56–110 m), zone III (111–185 m), and zone IV (186–366 m). Similarly, time of tow was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00 to 3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59). Bottom and surface temperatures were grouped into three zones based on the 25th (P_{25}) and 75th (P_{75}) percentiles of the empirical temperature distribution of each of these two variables. Temperature zone I was P_0 to P_{25}, zone II was P_{25} to P_{75}, and zone III was P_{75} to P_{100}. Mean catches between zones were compared after applying a logarithmic transformation to stabilize the variance of number per tow. Similarly, mean ratios of juvenile to adult catches were compared between zones after applying a logarithmic transformation to the ratio. Mean $\log_{10}$-transformed catch per tow values of juveniles and adults and their ratios were tested at the 5% level of significance by using the GT-2 test which is appropriate for unplanned comparisons with unequal sample sizes (Sokal and Rohlf, 1981). Only the effects of individual environmental factors on juvenile and adult catches were evaluated in these univariate tests and the potentially important factors of interannual changes in abundance or of survey stratification were subsumed into random variation.

Diel correction factors

We analyzed the combined effects of survey design, time of day, and annual squid abundance to determine correction factors for diel differences in catchability of juvenile and adult squid. As in the evaluation of size-specific environmental effects, catches (C) from tows that captured both juveniles and adults were $\log_{10}$-transformed. A general linear model (Searle, 1987) was applied to estimate the effects of survey stratum (Fig. 1), time of day category, and year on $\log_{10}$-transformed catches. Time of day was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00–3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59) so that the time period effect (T) measured diel differences in mean catch. The year effect (Y) provided a measure of the effect of changes in relative annual abundance on mean catch whereas the survey stratum effect (S) accounted for the effects of geographic location and depth. The general linear model (GLM) was

$$\log C_{ijk} = \log U_R + \log T_i + \log Y_j + \log S_k + \varepsilon_{ijk}, \quad (4)$$

where C_{ijk} = mean catch during the i^{th} time period (T_i) in the j^{th} year (Y_j) within the k^{th} stratum (S_k);

U_R = mean catch in a standard reference cell (where standard time period=day, year=1994, and survey stratum=1); and

ε_{ijk} = an independent and identically distributed normal random variable with zero mean and constant variance σ^2.

Parameters of the GLM model were estimated using ANOVA for both prerecruit and recruit catches of each species. The significance of time, year, and stratum effects were evaluated by using type-III sums of squares that do not depend on the order in which effects are added to the model (Searle, 1987). Because daytime was the reference time period, the diel coefficient for the daytime had the value 1. Point estimates and confidence intervals of time zone I (T_I) and II (T_{II}) coefficients in relation to the daytime coefficient were computed whenever the diel effect was significant. Given estimates of T_I and T_{II}, catches (y_{ih}) made during time zone I or II period can be corrected to daytime catch units by dividing them by the diel effects coefficient as y_{ih}/T_I and y_{ih}/T_{II}, respectively. Diel-standardized, stratified mean catches ($\bar{y}_{st}^*$) can be expanded by the total number of sampling units within the survey region (N) to provide minimum swept-area estimates of juvenile or adult population size ($N\bar{y}_{st}^*$) and variance ($N^2\ Var[\bar{y}_{st}^*]$) within the survey region using stratified random sampling estimators (Cochran, 1977).

Results

Within-year associations

The neritic squid species exhibited different degrees of within-year habitat associations than those exhibited by the oceanic species. Results of the randomization tests of *L. pealei* catches with depth, time of day, bottom temperature, and surface temperature (Table 1) showed that *L. pealei* catch was consistently associated with each of these factors. Associations were significant ($P<0.05$) in all years for depth, bottom temperature, and surface temperature. For time of day, associations were significant in all years except 1980 (96%). In contrast, results of the randomization tests for *I. illecebrosus* (Table 2) indicated that catches of this species were inconsistently associated with only some of the factors. During the 28 years analyzed, a total of 15, 13, 7, and 12 associations were significant for depth, time of day, bottom temperature, and surface temperature, respectively. All four factors were significantly associated with *I. illecebrosus* catch during 1983; otherwise, there was no apparent pattern of annual associations. Overall, *L. pealei* exhibited consistent within-year associations, whereas *I. illecebrosus* exhibited variable within-year associations with the four environmental factors.

We compared the interquartile range of the catch-weighted CDF of each factor to the interquartile range of its unweighted CDF to see how associations varied across years. For brevity, the term "midrange" denotes the "average interquartile range" in what follows. For depth, this comparison of CDFs showed whether *L. pealei* or *I. illecebrosus* preferred shallower or deeper water in relation to observed depths. The midranges of depth for *L. pealei* and *I. illecebrosus* catches were 37–75 m and 79–149 m (Fig. 2A), respectively, whereas the midrange of all observed depths was 51–166 m. For *L. pealei*, the average of the median catch-weighted depth was 50 m, about 35 m shallower than the average observed depth and equal to the P_{25} of the observed depths. In contrast, the average of the median catch-weighted

Table 1

Results of univariate randomization test of association between catches of *L. pealei* and depth, time of day, bottom temperature, and surface temperature, during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *L. pealei* catches and the environmental factor. The symbol "*" denotes probability values of $0.05 \geq P > 0.01$, and the symbol "**" denotes the probability values of $0.01 \geq P$.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.00**	0.00**	0.00**	0.00**
1968	0.00**	0.00**	0.00**	0.00**
1969	0.00**	0.00**	0.00**	0.00**
1970	0.00**	0.00**	0.00**	0.00**
1971	0.03*	0.00**	0.00**	0.00**
1972	0.00**	0.00**	0.00**	0.00**
1973	0.04*	0.00**	0.00**	0.00**
1974	0.00**	0.00**	0.00**	0.00**
1975	0.00**	0.00**	0.00**	0.00**
1976	0.00**	0.00**	0.00**	0.00**
1977	0.00**	0.00**	0.00**	0.00**
1978	0.00**	0.00**	0.00**	0.00**
1979	0.00**	0.00**	0.00**	0.00**
1980	0.00**	0.07	0.00**	0.00**
1981	0.00**	0.00**	0.00**	0.00**
1982	0.01**	0.00**	0.03*	0.00**
1983	0.01**	0.00**	0.00**	0.00**
1984	0.00**	0.00**	0.00**	0.00**
1985	0.00**	0.00**	0.00**	0.00**
1986	0.01**	0.00**	0.00**	0.00**
1987	0.00**	0.00**	0.00**	0.00**
1988	0.00**	0.02*	0.00**	0.00**
1989	0.00**	0.00**	0.02*	0.00**
1990[1]	0.00**	0.00**	0.00**	0.00**
1991	0.00**	0.00**	0.00**	0.00**
1992	0.00**	0.00**	0.00**	0.00**
1993	0.02*	0.01**	0.00**	0.00**
1994	0.00**	0.00**	0.00**	0.00**

[1] No bottom temperature data were collected on Georges Bank during 1990.

depth for *I. illecebrosus* was 106 m, roughly 20 m deeper than the average observed depth. Overall, *L. pealei* was consistently associated with shallow depths (37–75 m), whereas *I. illecebrosus* was more common in deeper waters (79–149 m).

The comparison of midranges for time of day indicated whether *L. pealei* or *I. illecebrosus* catches were more prevalent during night or day. We measured time in relation to a reference time of day (6:00 AM EST) because this roughly corresponds to first light, during autumn, when diel effects on the behavior of squid might be expected to change. This choice did not affect the results of the habitat association test; however, median time of day was 18:00 EST, instead of 12:00 noon EST. The midranges for time of day for *L. pealei* and *I. illecebrosus* catches were 10:00–17:00 EST and 10:00–18:00 EST, respectively (Fig. 2B). In comparison, the midrange for time of day was 13:00–1:00 EST. For both *L. pealei* and *I. illecebrosus*, the average median catch-weighted time of day was 14:00 EST, roughly 4 hours earlier than the average median time of 18:00 EST, and roughly equal to P_{25} of the overall time distribution. Overall, both *L. pealei* and *I. illecebrosus* exhibited diel catchability because squid catches were consistently greater during day than at night.

Potential effects of bottom temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler bottom temperatures. The midranges of bottom temperature for *L. pealei* and *I. illecebrosus* catches were 11–15°C and 9–13°C, respectively, and the midrange for bottom temperature was 8–13°C (Fig. 2C). For *L. pealei*, the average of the median catch-weighted bottom temperature was 13°C, about 3°C warmer than the average of the overall bottom temperature distribution. For *I. illecebrosus*, the average of the median catch-weighted bottom temperature was 11°C, which was nearly equal to the average of the observed bottom temperature distribution Although *L. pealei* was associated with warmer bottom temperatures, it did not appear that *I. illecebrosus* was closely associated with bottom temperature.

Effects of surface temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler surface temperatures. The midranges of surface temperature for *L. pealei* and *I. illecebrosus* catches were 17–20°C and 13–20°C (Fig. 2D), respectively, and the midrange for all surface temperatures was 11–19°C. For *L. pealei*, the average of the median catch-weighted surface temperature was 18°C; about 4°C warmer than the average overall surface temperature distribution. Similarly, the median catch-weighted surface temperature of 16°C for *I. illecebrosus* was 2°C warmer than this average. Overall, *L. pealei* was generally associated with warmer surface temperatures, whereas *I. illecebrosus* associations were more variable, and this species was less frequently associated with warmer surface temperatures.

Table 2

Results of univariate randomization test of association between catches of *I. illecebrosus* and depth, time of day, bottom temperature, surface temperature during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *I. illecebrosus* catches and the environmental factor. The symbol "*" denotes probability values of $0.05 \geq P > 0.01$, and the symbol "**" denotes the probability values of $0.01 \geq P$.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.13	0.01**	0.01**	0.00**
1968	0.03*	0.24	0.05*	0.01**
1969	0.08	0.03*	0.26	0.33
1970	0.16	0.15	0.02*	0.02*
1971	0.01**	0.01**	0.00**	0.08
1972	0.24	0.30	0.12	0.03*
1973	0.04*	0.13	0.71	0.12
1974	0.52	0.03*	0.03*	0.23
1975	0.34	0.00**	0.77	0.00**
1976	0.02*	0.20	0.54	0.30
1977	0.04*	0.44	0.26	0.01**
1978	0.12	0.00**	0.87	0.03*
1979	0.00**	0.15	0.07	0.07
1980	0.01**	0.01**	0.24	0.25
1981	0.61	0.01**	0.51	0.25
1982	0.03*	0.00**	0.09	0.18
1983	0.03*	0.00**	0.01**	0.00**
1984	0.03*	0.47	0.42	0.00**
1985	0.00**	0.00**	0.24	0.12
1986	0.03*	0.51	0.60	0.31
1987	0.39	0.34	0.53	0.04*
1988	0.98	0.12	0.06	0.34
1989	0.69	0.10	0.32	0.58
1990[1]	0.00**	0.00**	0.27	0.09
1991	0.04*	0.36	0.11	0.48
1992	0.13	0.01**	0.00**	0.00**
1993	0.33	0.24	0.53	0.03*
1994	0.04*	0.18	0.09	0.39

[1] No bottom temperature data were collected on Georges Bank during 1990

Size-specific environmental effects

Mean catches of *L. pealei* prerecruits and recruits varied across depth zones (Fig. 3A) where combined sample sizes for depth zones I, II, III, and IV were 1234, 1012, 270, and 99 tows, respectively. Mean catches of prerecruits peaked in zone I and declined

with depth, whereas mean catches of recruits peaked in zone III. The lowest mean catch of *L. pealei* prerecruits and recruits occurred in the deepest strata, zone IV. There was no significant difference between mean catches of prerecruits in depth zones II and III or recruits in zones I and II or zones II and III (Fig. 3A). The mean ratio of prerecruit to recruit catches was highest in depth zone I (Fig. 3B) and exhibited a declining trend with depth. However, the mean ratio was not significantly different in depth zones II, III, and IV. Overall, catches of *L. pealei* prerecruits decreased with depth, whereas recruit catches peaked at intermediate depths (111–185 m).

For *I. illecebrosus*, mean catches exhibited heterogeneity across depth zones (Fig, 3C), where sample sizes for depth zones I, II, III, and IV were 85, 283, 161, and 81 tows, respectively. Mean catches of recruits increased with depth and were highest in depth zone IV, whereas mean catches of prerecruits were relatively homogeneous across depths but were lowest in zone II. For prerecruits, mean catches were significantly different only between zones I and II (Fig. 3C). In contrast, mean catches of recruits were significantly different between all depth zones except zones III and IV and zones II and III. The mean ratio of prerecruit to recruit catches peaked in zone I, whereas the mean ratios in zones II, III, and IV were not significantly different (Fig. 3B). Overall, catches of *I. illecebrosus* prerecruits peaked in the shallowest depth zone (27–55 m) but were similar at greater depths. Similar to those of *L. pealei*, catches of *I. illecebrosus* recruits increased with depth as the ratio of prerecruit to recruit catch decreased with depth.

As expected, mean catch of *L. pealei* prerecruits and recruits peaked during day and were lowest at night (Fig. 4A). Sample sizes for time zones I, II, and III were 518, 968, and 1129 tows, respectively. For prerecruits, mean catch by time of day differed significantly for all three time zones (Fig. 4A), whereas mean catches of recruits were not significantly different between those for time zone II and zone III. The mean ratio of prerecruit to recruit catches peaked during day and was lowest at night (Fig. 4B), whereas the mean ratios for all time zones were significantly different (Fig. 4B). Overall, catches of both *L. pealei* prerecruits and recruits increased during day, although the difference between day and night catches was more pronounced for prerecruits.

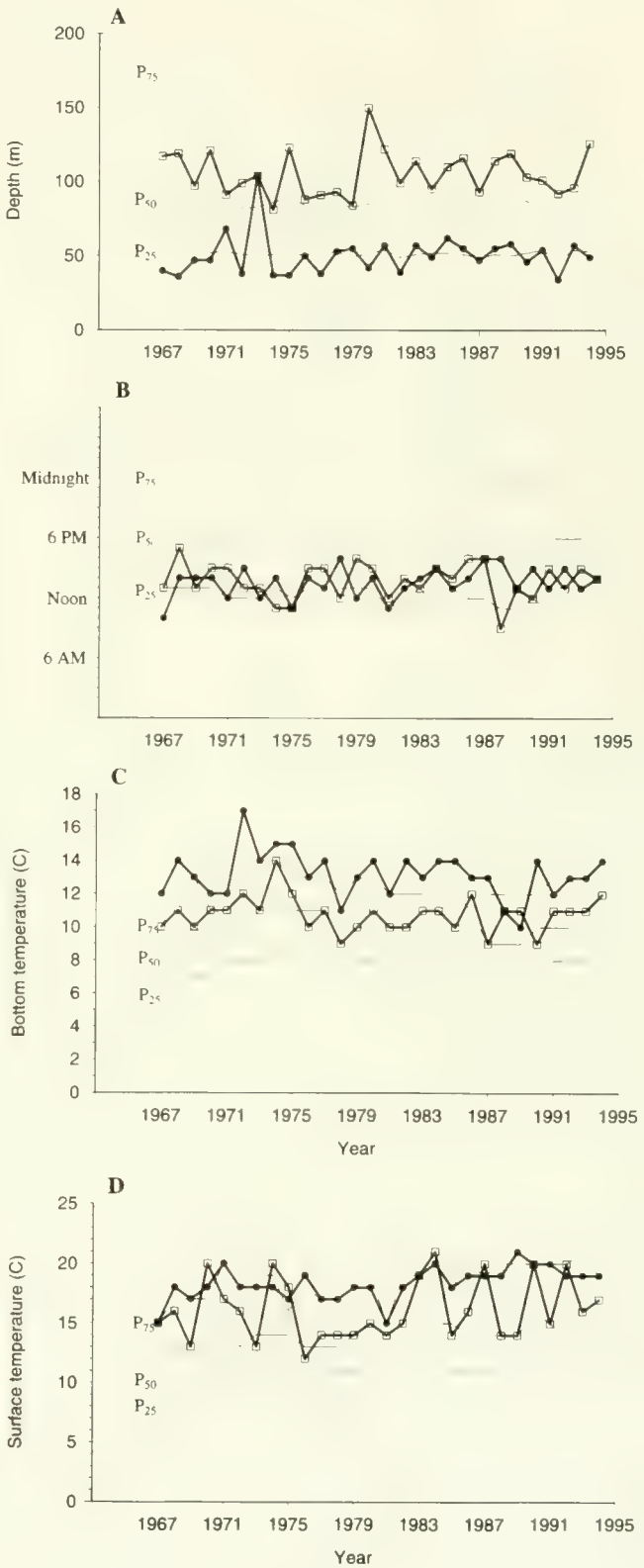

Figure 2

Catch-weighted averages of (**A**) depth (m), (**B**) time of day (h), (**C**) bottom temperature (°C), and (**D**) surface temperature (°C) by year for *L. pealei* (solid circle) and *I. illecebrosus* (open square). The 25th, 50th, and 75th percentiles (P_{25}, P_{50}, and P_{75}, thin solid lines) of the annual autumn distribution of each environmental factor are provided for comparison.

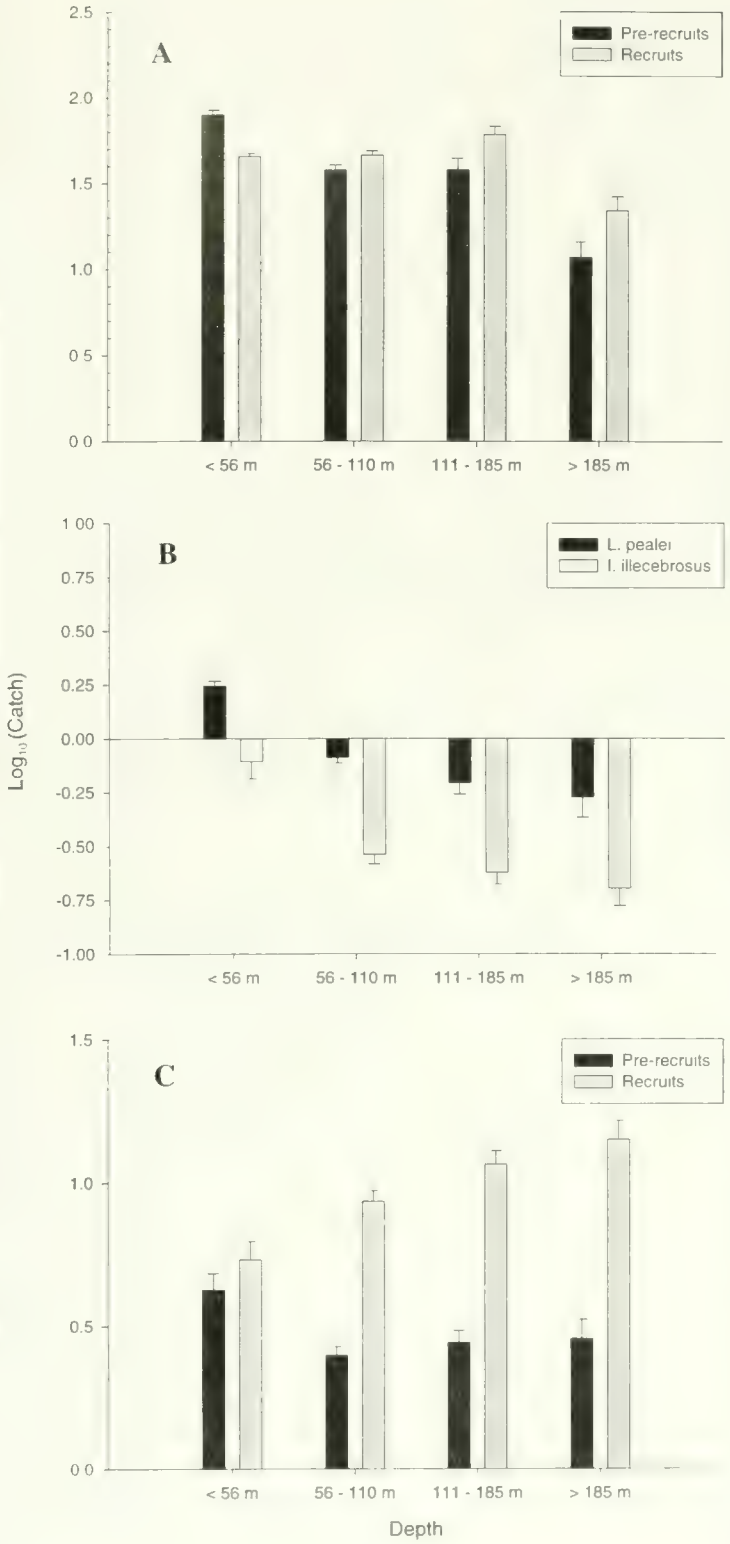

Figure 3

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by depth for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

For *I. illecebrosus*, the mean catch of prerecruits was highest during the day, whereas the mean catch of recruits peaked during dawn and dusk (Fig. 4C), where sample sizes for time zones I, II, and III were 86, 211, and 313 tows, respectively. Mean catches of prerecruits and recruits were lowest at night. For prerecruits, mean catches were not significantly different between time zones I and II (Fig. 4C). In contrast, mean catches of recruits were not significantly different between time zones II and III. Although the mean ratio of prerecruit to recruit catches peaked during the day (Fig. 4B), mean ratios were significantly different between time zones II and III. Similar to catches of *L. pealei*, catches of both size categories of *I. illecebrosus* were lowest at night.

Mean catches of *L. pealei* prerecruits and recruits differed by bottom temperature zone (Fig. 5A) where temperature zones I, II, and III were 5.5 to 10.9°C (n=604), 10.9 to 16.1°C (n=1,340), and 16.1 to 28.0°C (n=272), respectively. Mean catch of prerecruits increased with bottom temperature and peaked in the warmest zone, whereas mean catch of recruits was greatest in zones II and III. In contrast, the mean catches of both size categories were lowest in temperature zone I. Mean catches of prerecruits were significantly different between all bottom temperature zones (Fig. 5A), whereas mean catches of recruits were not significantly different between zones II and III. The mean ratio of prerecruit to recruit catch peaked in zone III (Fig. 5B), and the mean ratios were not significantly different between zones I and II. Overall, catches of *L. pealei* prerecruits increased with increasing bottom temperature, whereas catches of recruits peaked at intermediate levels (11–16 C).

Catches of *I. illecebrosus* prerecruits and recruits also varied (Fig. 5C) with bottom temperature, where zones I, II, and III were 5.1 to 10.2°C (n=122), 10.2 to 12.9°C (n=242), and 12.9 to 25.5°C (n=121), respectively. For *I. illecebrosus* prerecruits, mean catches were greatest in temperature zones I and II, and the mean catch of recruits peaked in zone II. Mean catches of *I. illecebrosus* prerecruits and recruits were lowest in temperature zones I and III,

respectively. For prerecruits, mean catches were significantly different only between temperature zones I and II (Fig. 5C), whereas mean catches of recruits were significantly different only between zones II and III. The mean ratio of prerecruit to recruit catches was greatest in temperature zones II and III (Fig. 5D), however there was no significant difference between the three zones. Overall, catches of *I. illecebrosus* prerecruits and recruits were relatively similar over the range of observed bottom temperatures (5–25°C).

Mean catches of *L. pealei* prerecruits and recruits differed with surface temperature (Fig. 6A) where temperature zones I, II, and III were 7.1 to 14.8°C (n=615), 14.8 to 20.9°C (n=1,178), and 20.9 to 28.3°C (n=460), respectively. Mean catches of prerecruits and recruits peaked in temperature zone II, whereas the lowest mean catch of prerecruits and recruits occurred in temperature zone I. Mean catches of both prerecruits and recruits were significantly different across all surface temperature zones (Fig. 6A). The mean ratio of prerecruit to recruit catches peaked in temperature zone II and the mean ratios were significantly different across all surface temperature zones (Fig. 6B). Overall, catches of *L. pealei* prerecruits and recruits peaked at intermediate surface temperatures (15–21°C).

Mean catches of *I. illecebrosus* prerecruits and recruits (Fig. 6C) also varied with surface temperature, where temperature zones I, II, and III were 7.8 to 14.4°C (n=123), 14.4 to 20.6°C (n=242), and 20.6 to 26.5°C (n=131), respectively. For *I. illecebrosus* prerecruits, mean catch peaked in temperature zone II but exhibited no trend across zones. In contrast, mean catch of recruits peaked in temperature zone III and exhibited an increasing trend with surface temperature. There were no significant differences in mean catch of prerecruits, by surface temperature zone (Fig. 6C), but mean catches of recruits were significantly different between temperature zones I and III. The mean ratio of prerecruit to recruit catch peaked in temperature zone I (Fig. 6D) and declined with increasing surface temperature. These mean ratios were significantly different between zones I and III. Over-

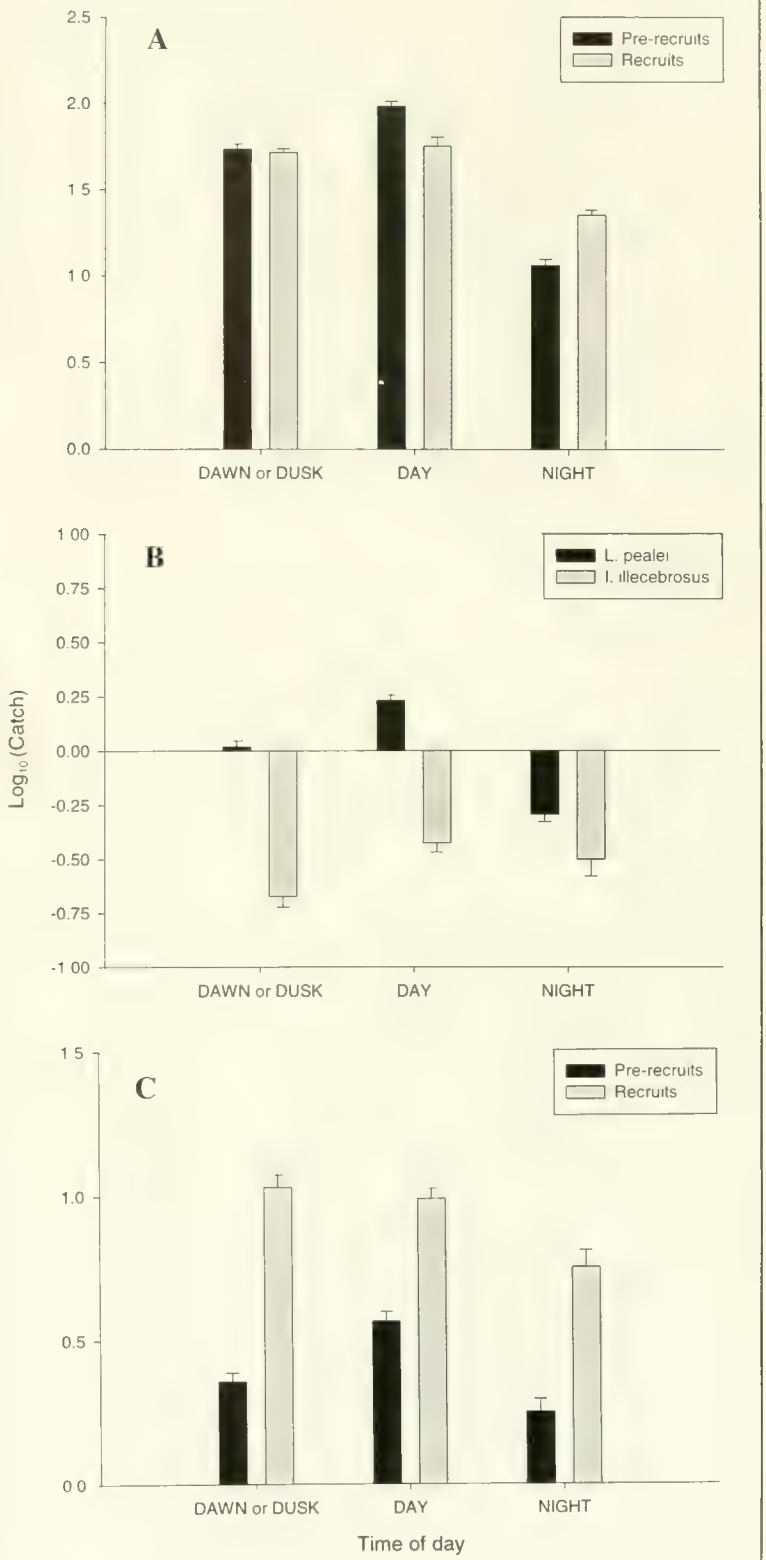

Figure 4

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by time of day for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

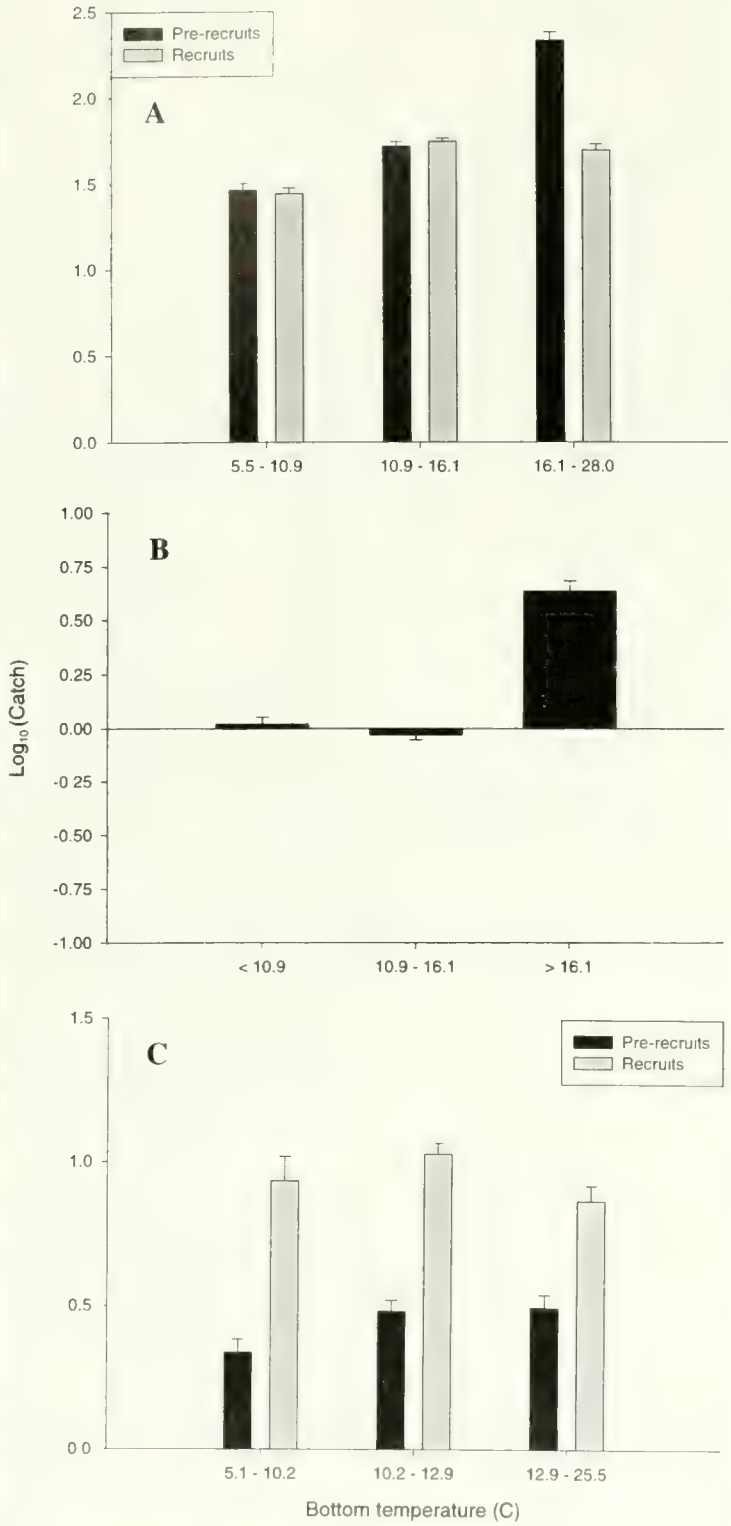

Figure 5

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by bottom temperature for positive catches of prerecruits and recruits.

all, catches of *I. illecebrosus* prerecruits were similar across the range of observed surface temperatures (8–26°C), whereas catches of recruits increased with surface temperature.

Diel correction factors

Diel effects from the GLM analyses were significant for *L. pealei* prerecruits and recruits and for *I. illecebrosus* prerecruits (Table 3). For *L. pealei* prerecruits, the time period effect was highly significant (F_S=280.79, P<0.001), and the year (F_S=6.05, P<0.001) and stratum effects (F_S=16.23, P<0.001) were also significant. Estimates of the diel effects coefficients for *L. pealei* prerecruits were T_I = 0.0873 with 95% CI of [0.0713, 0.1068] and T_{II} = 0.4654 with 95%CI of [0.3958, 0.5472]. For comparison, daytime catch rates of *L. pealei* prerecruits were roughly were about 11.5 times higher than time zone I values and 2.1 times higher than time zone II values. Similarly, for *L. pealei* recruits, the time period effect was highly significant (F_S=100.06, P<0.001), and the year (F_S=9.84, P<0.001) and stratum (F_S=12.45, P<0.001) effects were also significant. Estimates of the diel effects coefficients for *L. pealei* recruits were T_I = 0.3420 with 95% CI of [0.2939, 0.3979] and T_{II} = 0.8325 with 95%CI of [0.7372, 0.9402]. Time zone III catch rates of *L. pealei* recruits were roughly 2.9 times higher than time zone I values and about 1.2 times higher than zone II values. For *I. illecebrosus* prerecruits, the time period effect was significant (F_S=20.23, P<0.001). The stratum effect was also significant (F_S=1.98, P<0.001) but the year effect was not (F_S=1.48, P=0.057). Diel effects coefficients were estimated to be T_I = 0.4251 with 95% CI of [0.3158, 0.5724] and T_{II} = 0.6281 with 95%CI of [0.5093, 0.7746]. By comparison, time zone III catch rates of *I. illecebrosus* prerecruits were about 2.4 times higher than zone I values and roughly 1.6 times higher than time zone II values. For *I. illecebrosus* recruits, the time period effect was not significant (F_S=2.25, P=0.106), although the year (F_S=5.41, P<0.001) and stratum (F_S=3.05, P<0.001) effects were significant. For both species, diel effects were more pronounced for prerecruits than for recruits.

Discussion

We found that *L. pealei* was consistently associated with all the environmental factors examined. The habitat associations of *L. pealei* with depth, bottom temperature, and surface temperature indicated that these factors were important determinants of its autumn distribution. The consistent association of *L. pealei* with time of day appeared to be a consequence of the behavioral ecology of the species as it moves upward in the water column during the night to avoid predation or to acquire prey.

In comparison with *L. pealei*, autumn survey catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. For many of the years examined, *I. illecebrosus* catches were not associated with depth, temperature, or time of day. *Illex illecebrosus* feeds opportunistically in continental shelf waters from Newfoundland to Cape Hatteras, during summer and autumn, prior to undertaking a lengthy offshore migration to spawning areas south of Cape Hatteras (O'Dor and Dawe, in press). Therefore, the lack of consistent habitat associations may be partly due to incomplete survey coverage of *I. illecebrosus* habitat during autumn and a lack of availability of this species to the bottom trawl survey gear. For example, the timing of the offshore and southward migration of *I. illecebrosus* may precede rather than follow the timing of the autumn survey in some years. In addition, few stations are sampled in the autumn habitat of this species, at the shoreward edge of the convergence zone, and these low sample sizes may make it difficult to detect habitat associations. Nevertheless, *I. illecebrosus* catches were significantly associated with depth, time of day, and surface temperature in approximately half of the years examined. Depth and surface temperature may be determinants of preferred habitat of *I. Illecebrosus;* however the importance of these factors varied between years. The significant association of *I. illecebrosus* catches with daylight indicated that the species undertakes vertical migrations similar to those of *L. pealei*, but with less regularity as might be expected of an ommastrephid (Roper and Young, 1975).

Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches. This association with depth corroborated previous studies. Serchuk and Rathjen (1974) examined the distribution and relative abundance of *L. pealei* and found that the highest catches were at depths less than 100 m during autumn. Vovk (1978) reported that the primary depth range of *L. pealei* was 50–100 m during September–November, and Lange and Sissen-

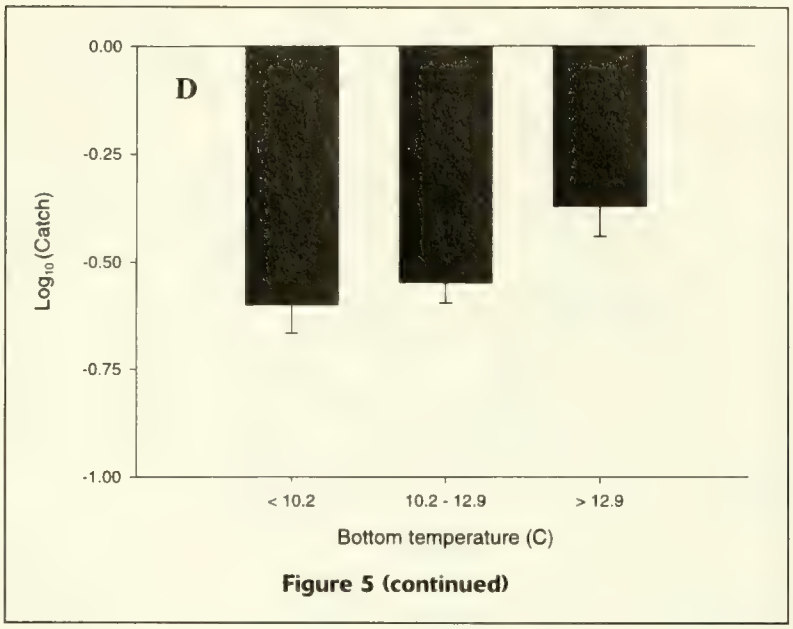

Figure 5 (continued)

Table 3

Analysis of variance tables for general linear model results to estimate diel correction factors for *L. pealei* and *I. illecebrosus* prerecruits and recruits, where df is degrees of freedom, SS is type-III sums of squares, MS is mean square, F_S is the *F*-statistic, and *P* is the probability value.

Source of variation	df	SS	MS	F_S	*P*
L. pealei prerecruits					
Year	27	104.824	3.882	6.05	<0.001
Stratum	50	520.624	10.413	16.23	<0.001
Time of day	2	360.353	180.176	280.79	<0.001
L. pealei recruits					
Year	27	96.171	3.562	9.84	<0.001
Stratum	50	225.257	4.505	12.45	<0.001
Time of day	2	72.439	36.220	100.06	<0.001
I. illecebrosus prerecruits					
Year	27	9.761	0.362	1.48	0.057
Stratum	50	24.114	0.482	1.98	<0.001
Time of day	2	9.866	4.933	20.23	<0.001
I. illecebrosus recruits					
Year	27	41.351	1.532	5.41	<0.001
Stratum	50	43.274	0.865	3.05	<0.001
Time of day	2	1.275	0.637	2.25	0.106

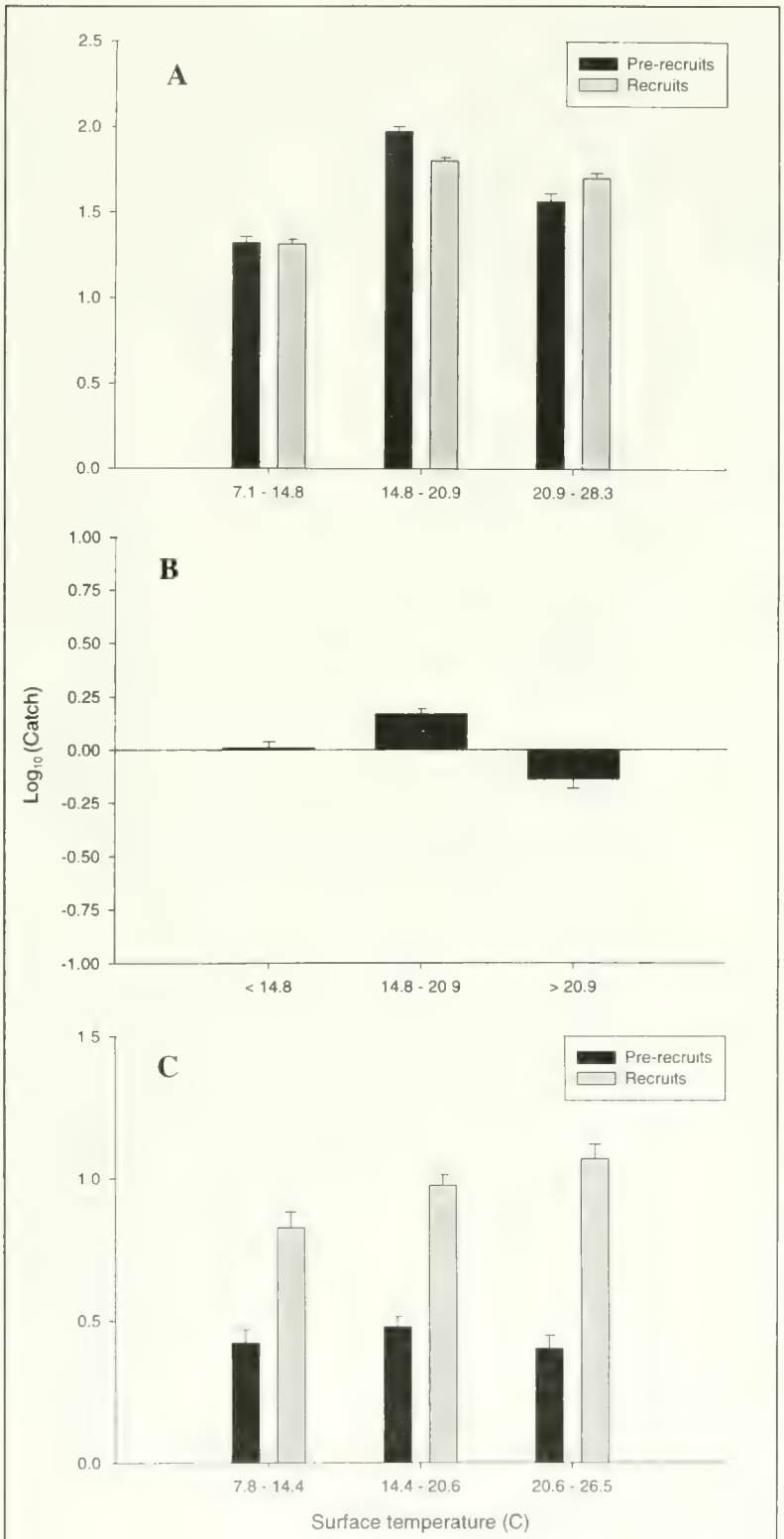

Figure 6

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by surface temperature for positive catches of prerecruits and recruits.

wine (1983) reported relatively high catches at shallow (27–55 m) and also intermediate depths (111–185 m). In this study, however, depth affected catches of juvenile and adult *L. pealei* differently. Most shallow-water catches comprised juveniles, and this finding indicated that nearshore waters of the continental shelf constitute a preferred habitat of *L. pealei* juveniles during autumn. Catches of juveniles also decreased at greater depths. In contrast, catches of *L. pealei* adults peaked at depths near the edge of the continental shelf. We detected a bathymetric pattern of larger *L. pealei* with increasing depth. This pattern was also reported by Vovk (1978) on the basis of distant water fleet catches of *L. pealei* and is similar to the ontogenetic descent reported for some other loliginids (*L. gahi*, Hatfield et al., 1990; *L. vulgaris reynaudii*, Augustyn et al., 1992).

In comparison with *L. pealei*, the effect of depth on *I. illecebrosus* was similar but less pronounced. This difference was probably due to the fact that *I. illecebrosus* utilize a wider range of depths than do *L. pealei* as they feed in shallow nearshore areas and undertake long distance migrations in continental slope waters (O' Dor and Dawe, in press). Nonetheless, the empirical patterns of *I. illecebrosus* catches in relation to depth in our study area were consistent with those from different areas. In particular, Whitaker (1980) reported that *I. illecebrosus* catches were relatively low at depths less than 56 m and peaked at depths between 186 and 366 m in waters south of Cape Hatteras, whereas Grinkov and Rikhter[3] reported that *I. illecebrosus* catches peaked at depths of 100–150 m along the edge of the continental shelf off Nova Scotia. In our study, much of the *I. illecebrosus* catch occurred at depths of roughly 80–150 m. As with *L. pealei*, we found that depth affected the catch of *I. illecebrosus* juveniles and adults differ-

[3] Grinkov, Y. A., and V. A. Rikhter. 1981. Some data on distribution of groundfish and short-finned squid along the oceanic slopes of the Scotian Shelf in spring, 1979. Northwest Atlantic Fisheries Organization (NAFO) SCR Doc. 81/VI/63, ser. no. N347, 13 p.

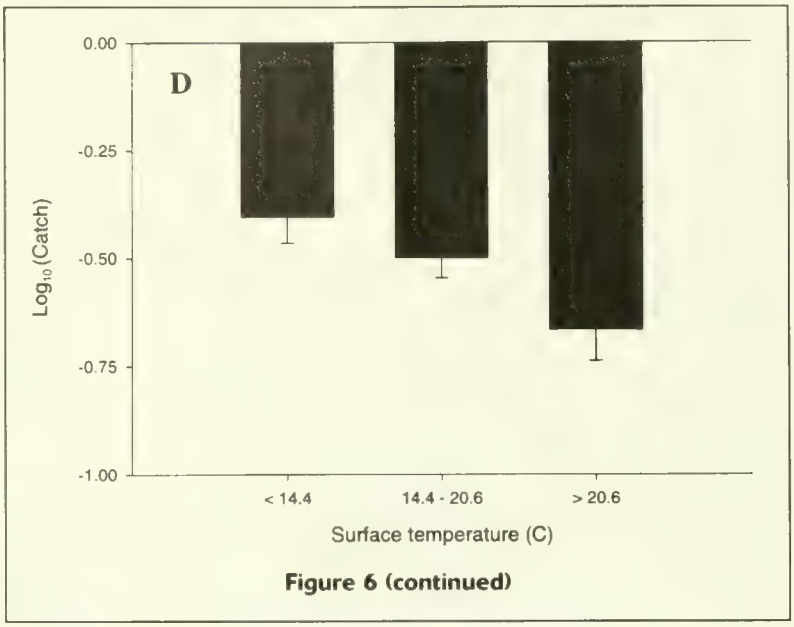

Figure 6 (continued)

ently. Catches of juveniles decreased at greater depths, and there was a bathymetric pattern of larger *I. illecebrosus* with increasing depth. Although catches of adults increased with depth, in contrast with *L. pealei*, catches of *I. illecebrosus* adults peaked at depths of 186–366 m. This depth range corresponds to the convergence zone between continental shelf and slope waters and intersects the shelf edge at roughly 150–200 m (Bowman, 1977). Commercial fishery catch data were consistent with this observation, as Lange, Ingham, and Price[4] reported, noting that the highest catch rates recorded by domestic observers in the distant-water *I. illecebrosus* fishery were generally located within several miles of the shelf-slope front, at the shoreward edge of the convergence zone, between continental shelf and slope water. Overall, these observations suggested that the shelf-slope convergence zone is an important habitat for adult *I. illecebrosus* during autumn.

Our analyses also demonstrated the importance of diel effects on *L. pealei* catches. This generally corroborated previous observations. Summers (1968) observed that *L. pealei* migrated vertically and that squid could be observed near the surface at night. Summers (1969) and Lange and Sissenwine (1983) observed that survey catches of *L. pealei* during the day were consistently higher than catches at night. Serchuk and Rathjen (1974) observed that 90% of *L. pealei* survey catches occurred during daylight, and Sissenwine and Bowman (1978) found that *L. pealei* catches were significantly higher during day. In our study, significant differences in diel effects were detected for both juveniles and adults. Catches of *L. pealei* juveniles and adults increased with increasing light availability although the diel effects were more pronounced for juveniles. In particular, time zone I and II catches of juveniles were 92% and 54% below mean catch during the day, whereas zone I and II catches of adults were 66% and 17% lower. The fact that the diel effect was more pronounced for juvenile *L. pealei* may be related to differences in feeding behavior between juveniles and adults. *L. pealei* hatchlings must feed near the surface until their tentacles develop and they can capture larger prey (Vecchione, 1981) whereas adults are primarily demersal and commonly rest on the bottom (Hanlon et al., 1983). Small juveniles feed primarily on crustaceans and gradually shift to a more diverse diet of crustaceans, fish, and squid as they grow and can capture larger and more energetically valuable prey (Vovk, 1972; Macy, 1982; Vovk, 1985; Anderson and Griswold, 1988). As a result, juveniles need to undertake vertical migrations at night more frequently to capture a sufficient amount of suitable prey.

The fact that *I. illecebrosus* catches were moderately associated with time of day was consistent with Sissenwine and Bowman (1978) and Shepherd and Forrester[2] who found that time of day had an important effect on catches of *I. illecebrosus*. Diel vertical migrations may be related to *I. illecebrosus* feeding activity. Vinogradov and Noskov (1979) found that the feeding intensity of this species is greatest at night and lowest during the day. Similar to catches of *L. pealei*, catches of *I. illecebrosus* were higher during day, and diel effects were more important for juveniles than adults. In particular, catches of juveniles at night and those at dawn and dusk were 37% and 57% below mean catch during the day. Guided by a review of the NEFSC domestic sea sampling program database, fishermen targeting *I. illecebrosus* take advantage of the behavior of this species by fishing only between dawn and dusk, when the squid are available to commercial bottom trawl gear. Schools of *I. illecebrosus* are not targeted at night because they are too dispersed near the surface of the water column. Instead schools of *I. illecebrosus* are targeted beginning at dawn, when they can be

[4] Lange, A. M. T., M. C. Ingham, and C. A. Price. 1984. Distribution of maturing *Illex illecebrosus* relative to the shelf-slope water front of the northeastern United States. NAFO SCR Doc. 84/IX/109, Ser. No. N906, 18 p.

consistently seen on sonar returning to the seabed.[5] In contrast, the ratios of juvenile to adult catches of *I. illecebrosus* were considerably lower than those for *L. pealei*. In part, this difference in ratios between species may reflect the importance of cannibalism for larger *I. illecebrosus* adults during autumn (O'Dor and Dawe, in press). Although diel effects on *I. illecebrosus* juvenile catches were similar to *L. pealei*, they were less consistent.

We found that bottom temperature had a significant effect on catches of *L. pealei* juveniles and adults. This generally corroborated prior studies. In particular, Summers (1969) observed that large catches of *L. pealei* during winter were restricted to bottom temperatures of 8°C or higher. This lower temperature limitation was supported by Serchuk and Rathjen (1974) and Vovk (1978) who reported that the majority of *L. pealei* catches during autumn occurred at bottom temperatures of roughly 9–14°C. Similarly, in our study, much of the *L. pealei* catch occurred at 11–15°C. However, catches of *L. pealei* juveniles were highest when bottom temperatures exceeded 16°C, whereas catches of adults were highest when bottom temperatures were 11–16°C. Our results suggest that *L. pealei* juveniles generally prefer warmer bottom temperatures than do adults that appear to prefer intermediate bottom temperatures. This difference in temperature preference might be expected if minor differences in temperature have a substantial impact upon growth rates of young squid (Forsythe, 1993).

In contrast to bottom temperature, catches of *L. pealei* juveniles and adults had a similar pattern with respect to surface temperature. The highest catches of both *L. pealei* juveniles and adults occurred at temperatures of 15–21°C, whereas catches were lowest for temperatures below 15°C. Although *L. pealei* catches might be expected to increase with warmer water temperatures, adult catches peaked at intermediate bottom and surface temperatures and then declined at higher temperatures. This decline suggested that the higher temperature ranges observed in the survey were not optimal for *L. pealei* adults. Overall, the strong association of *L. pealei* with water temperature suggested that annual variation in patterns of ocean temperature affects the distribution and influences growth and survival of this neritic species.

In comparison to *L. pealei*, the less frequent associations of *I. illecebrosus* catches with bottom and surface temperatures suggested that temperature has a variable influence on the distribution of *I. illecebrosus* from Cape Hatteras to the Gulf of Maine. Other studies generally supported the notion that *I. illecebrosus* are distributed over a broad range of temperatures. In particular, Whitaker (1980) reported that *I. illecebrosus* catches occurred over a wide range of bottom temperatures of 7–27°C, but that roughly 80% of the catch was taken in 8–10°C waters. Murawksi (1993) examined the mean latitudinal occurrence of *I. illecebrosus* in relation to bottom and surface temperatures during autumn NEFSC bottom trawl surveys but found no statistically significant relationship. Rowell et al. (1985b) reported that *I. illecebrosus* appear to prefer bottom temperatures in excess of 6°C during summer on the Scotian Shelf, but that temperature did not appear to be a limiting factor. In the present study, much of the *I. illecebrosus* catch occurred at bottom temperatures of 9–13°C and surface temperatures of 13–20°C. In comparison to *L. pealei*, *I. illecebrosus* appeared to prefer cooler bottom temperatures and surface temperatures. However, in contrast with *L. pealei*, bottom temperature had a similar affect on catches of juvenile and adult *I. illecebrosus*. Surface temperature affected catches of juveniles and adults differently and, in particular, adult *I. illecebrosus* catches increased with surface temperature. Overall, *I. illecebrosus* catches occurred over a broader range of water temperatures in comparison with *L. pealei*, as might be expected of an oceanic species with a range that extends from temperate to boreal waters.

Because the bottom trawl gear used on the NEFSC autumn survey only fishes 3.2 m above the seabed, diel differences in squid catches are expected when squid migrate vertically to acquire prey or to avoid predators. Significant differences were detected between catches by time of day for both juvenile and adult *L. pealei*. As a consequence, it was inferred that diel correction factors were appropriate for survey catches of this neritic species. In contrast, diel effects on survey catches of adult *I. illecebrosus* were not significant and diel correction factors were not developed for this oceanic species. The diel catchability of *L. pealei* presents some challenges for the analysis and interpretation of bottom trawl survey data to estimate squid population totals. On one hand, diel correction factors developed in this study can be applied to time zone I and II catches to provide a stratified mean catch per tow adjusted to daylight units. Resampling techniques, such as mirror-match bootstrapping, could be applied to estimate its variance (Smith, 1997) under appropriate distributional assumptions. In this case, all survey data could be used at the expense of additional computational cost and potential bias induced by applying the diel correction factors to all survey strata. On

[5] Goodwin, G. 1997. Captain of *F/V Relentless* and *F/V Persistence*. Davisville, Rhode Island, 02882. Personal commun.

the other hand, squid population size and its variance could be calculated on the basis of only daylight tows in the standard manner. In this case, roughly 1/3 of the available survey data would be used owing to the exclusion of time zone I and II tows. As a result, some survey strata would be undersampled and precision would be lower. In general, the trade-off between bias due to diel correction and loss of precision due to use of only daylight tows warrants further study.

Differences between *L. pealei* and *I. illecebrosus* catches by depth suggest that the stratification of the NEFSC bottom trawl survey, which was designed to sample groundfish populations, is appropriate for both species. Differences in *L. pealei* and *I. illecebrosus* catches by temperature imply that preferred temperature ranges likely exist for both species within the survey region. However, temperature would not be a useful stratification variable for analysis of squid catches because temperature strata are dynamic and would fluctuate each year and because such a variable would lead to overstratification given the current depth and geographic stratification of the NEFSC survey. Regardless of how temperature affects survey catches of squids, the growth, recruitment, and abundance of *L. pealei* and *I. illecebrosus* can be expected to vary with ocean temperature regime (e.g. Dawe and Warren, 1993; Brodziak and Macy, 1996) because both are ecological opportunists with high, intrinsic population growth rates. Understanding how environmental factors, such as temperature, influence the productivity and distribution of squid stocks remains an important topic for fisheries research and management.

Acknowledgments

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Modeling the dynamics of eastern rock lobster, *Jasus verreauxi*, stock in New South Wales, Australia

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Abstract.—Rock lobster, *Jasus verreauxi*, have been fished off New South Wales, Australia, since the late nineteenth century. Since 1994–95 (1 July 1994 to 30 June 1995) the fishery has been managed under an output-control scheme with an annual total allowable catch (TAC) of 106 metric tons (t). Estimates of catch and catch per unit of effort (CPUE) have been developed from data collected from the commercial fishery for the period 1903–1936 and the period from 1969–70 to 1993–94. A production model was fitted to these data by using a robust observation-error estimator that minimizes the median of squared differences between log-observed and predicted CPUEs. A bootstrap resampling procedure was incorporated into this robust estimation method to estimate stock parameters and their uncertainties. The virgin biomass of the rock lobster was 4084 t (its 5th and 95th percentiles being 2553 and 6400 t). The stock biomass decreased substantially until 1990–91. Since 1992–93, it has stabilized and has probably increased owing to the large decrease in the allowable catch after 1988–89. The stock biomass in year 1995–96 was likely to have been between 15% and 30% of the virgin biomass (75% confidence interval). The implications from using different estimation methods on assessing this lobster stock are discussed.

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The eastern rock lobster, *Jasus verreauxi*, reportedly is the largest spiny rock lobster in the world (Philips et al., 1980). It occurs in waters off the coast of New South Wales (NSW), Australia, around the coast of Tasmania, and as far west as South Australia (Montgomery, 1995). It is also found off New Zealand, predominantly around the North Island (Kensler, 1967a).

Limited information on the life history of *J. verreauxi* in waters off NSW is available (McWilliam and Philips, 1987; Montgomery, 1992, 1995; Montgomery and Kittaka, 1994; Montgomery[1]). Most information comes from studies of the species in waters off New Zealand (Kensler 1967a, 1967b, 1967c; Booth, 1984a, 1984b, 1986). However, comparisons of mitochondrial DNA from juvenile rock lobsters from NSW and New Zealand waters have suggested that the populations are genetically distinct (Brasher et al., 1992).

The distribution of rock lobsters across habitat is patchy. From the puerulus to early juvenile stages of their life cycle, lobsters are probably asocial and thought to occur principally within the complex structure of forests of macroalgae or within beds of seagrass in waters from the intertidal zone to 30 m. During the older stages of the juvenile phase, the animal may begin to aggregate and migrate en masse to the habitat of adults. Adult rock lobsters live in aggregations from depths of around 10 m to those of the continental slope (Montgomery, 1995; Montgomery[1]). From the older juvenile stage onward, lobsters aggregate by day, and at night they roam alone. Information on the movements of tagged rock lobsters off New Zealand (Booth, 1984b) and spatial patterns in the length composition of rock lobsters in waters off NSW (Montgomery[1]) suggest that for management purposes the entire NSW population of rock lobsters should be considered as a unit stock. These studies indicate that older juveniles and adults move in an inshore–offshore direction and along the coast. The movement along the coast is thought to be associated with breeding (Booth, 1984b).

Rock lobsters have been fished off the east coast of Australia since the late nineteenth century. It is an important fishery in NSW, with an annual output of over 5 million US dollars. Since the 1994–95 fishing

[1] Montgomery, S. S. 1990. Preliminary study of the fishery for rock lobsters off the coast of New South Wales. Final Report, grant no. 86/64. Fisheries Research and Development Corporation, Canberra, Australia, 166 p.

year (i.e. from July 1 1994 to June 30 1995), this fishery has been managed under an output-control scheme with an annual total allowable catch (TAC) of 106 t. No attempt has been made previously to quantify the dynamics of this fishery.

Abundance indices, catch per unit of effort (CPUE), have been developed by Montgomery (1995) from data collected in the commercial fishery for the period of 1903–36 and that from 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94. Because data are mainly collected and derived from the NSW commercial fishery, large errors are likely to exist in the catch and CPUE data, and there is a concern that the quality of the data is perhaps not good for the purpose of modeling.

Production models are fitted to catch and CPUE data by using an observation-error estimator that minimizes the sum of squared differences between log-observed and predicted CPUEs (Hilborn and Walters, 1992). This estimator assumes that there is only error in the observed abundance index and that there are no observation errors in catch or process errors in the dynamics of the stock biomass. Because the least-squares method is sensitive to the assumption on the error structure in the model (Rousseeuw and Leroy, 1987), the unrealistic error assumption associated with the observation-error estimator tends to result in large errors in estimated parameters when models are fitted to data (Schnute, 1989; Chen and Andrew, 1998).

A more realistic error structure should include process error in the dynamics of the stock biomass and observation errors in both CPUE and catch. In our case, if the distribution of all error terms can be fully defined, we can apply the Kalman filter to generate a likelihood function and then maximize this likelihood function to yield parameter estimates (Sullivan, 1992), or we can define an appropriate variance-covariance matrix based on the defined error structure and then apply a generalized least-squares method to estimate parameters in the model (Paloheimo and Chen, 1996). However, the former approach is rather complicated because the dynamic model is nonlinear and there are two observation models (i.e. one for CPUE and the other for catch; Reed and Simons, 1996). The latter approach needs information on process and observation errors (Paloheimo and Chen, 1996). Such information is probably nonexistent in most fisheries. Moreover, the parametric assumption on error distribution (e.g. normal, log-normal, etc) may not be true.

Because of all these difficulties with the error structure for production models, it is desirable to have an estimation method that is robust with respect to assumptions concerning model error structure. Least median of squared errors (LMSE; Rousseeuw, 1984), which minimizes the median of squared differences between predicted and observed log CPUEs, is such an estimator (Chen and Andrew, 1998). A bootstrap procedure (Efron, 1979) was incorporated into the LMSE estimator to estimate the parameters and their uncertainties in this study. The probability of short-term overexploitation, defined as a fishing mortality rate higher than the selected biological reference points, was estimated for the next fishing season with different levels of TAC.

Production models

Production models are the simplest stock assessment models that are commonly used in fisheries (Hilborn and Walters, 1992). The input data for these models are the time series of catch and associated abundance index. Several variants of production models have been proposed (e.g. Pella and Tomlinson, 1969; Walters and Hilborn, 1976; Schnute, 1977, 1989; Punt, 1993). Without considering the structure of observation and process errors, the deterministic production model that is most commonly used can be written as

$$B_{t+1} = B_t + g_t - C_t, \quad (1)$$

where B_t = the stock biomass;
C_t = the catch; and
g_t = the growth of population in biomass, all in year i.

The g_t is often referred to as surplus production and often described by the logistic or Schaefer function written as $g(B_t) = rB_t(1 - B_t/K)$, where r is a parameter describing the intrinsic rate of population growth in biomass and K is a parameter corresponding to the unfished equilibrium stock size (often referred to as the carrying capacity or virgin biomass). The stock biomass in year i is often assumed to be directly related to a relative abundance index that can be observed in fisheries. This assumption can be written as

$$I_t = qB_t,$$

where q = the catchability coefficient; and
I_t = the abundance index in year i (Hilborn and Waters, 1992).

Methods for the parameter estimation

The use of an appropriate method to fit a production model to the observed data has been shown to be as

important in terms of the reliability of estimated parameters as the specification of the algebraic form of the underlying population dynamic model (Punt, 1988, 1993; Polacheck et al., 1993). Several approaches have been proposed to estimate parameters in production models when only indices of abundance and catch are available (Hilborn and Walters, 1992). The four most commonly used approaches are equilibrium estimators (Gulland, 1961), effort-averaging estimators (Fox, 1975), process-error estimators (Walters and Hilborn, 1976; Schnute, 1977), and observation-error estimators (Butterworth and Andrew, 1984; Ludwig and Walters, 1985). These approaches differ in how observation and process errors are introduced into the models that describe the dynamics of populations.

Recently, it has been suggested in some studies that observation-error estimators tend to perform better than others in parameter estimation (Punt, 1988, 1993; Hilborn and Walters, 1992; Polacheck et al., 1993). These estimators are constructed by assuming that the population dynamic equations are deterministic (thus there is no process error) and that all of the error occurs in the relationship between stock biomass and relative abundance index. This assumption can be written as

$$\log(I_t) = \log(qB_t) + e_t.$$

With the assumption that the e_t are independent, normally distributed variates, the estimates of the model parameters ($B_{initial}$, q, r, and K) are obtained by maximizing the appropriate likelihood function (Polacheck et al., 1993) or by minimizing the sum of squared e_t (Hilborn and Walters, 1992). The time series of stock biomass are estimated by projecting the biomass at the start of the catch series forward by using the historical annual catches. Because the estimation methods for observation-error estimators are least-squares types, they are sensitive to the assumption about the error structure of the model. Thus, parameter estimates tend to be unreliable if the specification of error structure (i.e. no process error, no error in observed catch, and log-normal error in observed abundance index) is not correct. However, in practice, it is almost impossible to know the true error structure. It is therefore desirable to use an estimation approach that is robust to the assumption about the model error structure for observation-error estimators.

An observation-error estimator, which minimizes the median of squared differences between observed and predicted log CPUEs, has been found to be robust with respect to incorrect specification of error structure (Chen and Andrew, 1998). This estimator can be written as

$$Minimize \underset{i=1,\ldots,N}{median} \left[\log(I_i) - \log(\hat{I}_i)\right]^2.$$

It is an extension of the linear robust regression method used by Chen and Paloheimo (1994) and Chen et al.(1994) for nonlinear parameter estimation. It should be noted that the algorithm developed for the linear parameter estimation (Rousseeuw, 1984) can not be used for the above estimator. The simplex method of Nelder and Mead (1965) was used to conduct the nonlinear parameter estimation for the above estimator (Press et al., 1992; Chen and Andrew, 1998).

Estimation of stock parameters for eastern rock lobster

Catch and CPUE data were available for two time periods. The first period (hereafter referred to as period I) was from 1903 to 1936, and the second (period II) from 1969–70 to 1993–94. The fishery was confined to grounds close to shore in period I, whereas from the beginning of period II, the fishery expanded to the continental slope. Therefore, it is highly likely that large differences in catchability existed between these two periods. Both the size and structure of the rock lobster stock on the NSW coast may have changed greatly over the two periods (Montgomery, 1995), and it is likely that the growth rate of the NSW rock lobster stock differed between these two periods of time. Parameters r and q were thus assumed to be different in these two time periods. Parameter K was assumed to be the same for these two time periods. This assumption was considered to be reasonable because the harvesting on the expanded fishing grounds at the beginning of period II was not from an unexploited portion of the stock. It is thought that eastern rock lobsters along the NSW coast display a movement that is typical of several other species of rock lobster, moving between inshore and offshore grounds and along the coast (see Herrnkind et al., 1994). Hence, lobsters on the grounds on the continental slope likely had been exposed to fishing on more traditional shallower grounds at other times.

The LMSE method was applied to fit the model to data observed in period I and estimate parameters B_{1903}, r_{I}, q_{I}, and K_{I}, where subscript I refers to period I. Because the year 1903 was early in the development of the fishery, it is reasonable to assume that B_{1903} is the same as K_{I} in parameter estimation (Hilborn and Walters, 1992). Thus, there are only three parameters to be estimated with data observed in the first time period.

An algorithm that incorporates a bootstrap approach into the LMSE method was developed to es-

timate the sampling distribution for model parameters. This approach is referred to as the bootstrapped LMSE method and its precedure follows:

1 estimate the model parameters using the LMSE method;
2 calculate the predicted CPUEs using the LMSE-estimated parameters;
3 calculate the residuals between observed and predicted log CPUEs;
4 randomly sample the residuals with replacement to add to the predicted logarithm CPUEs to yield pseudo observed CPUEs;
5 apply the LMSE algorithm to the pseudo observed CPUEs to estimate bootstrapped estimates;
6 repeat steps 4 to 5 100 times to simulate 100 sets of pseudo CPUE data and to estimate subsequently the corresponding 100 sets of bootstrapped parameters; and
7 calculate the median value and 90% confidence intervals for each parameter using the 100 bootstrapped estimates.

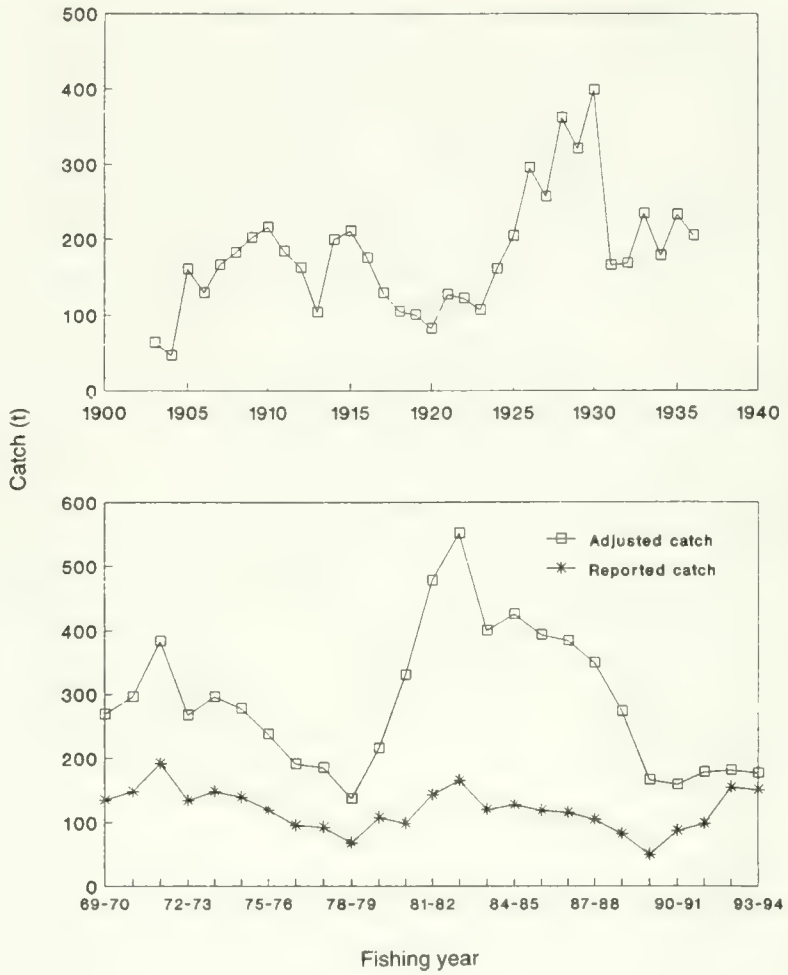

Figure 1

The landed catch of eastern rock lobsters in New South Wales (NSW), Australia, during the period of 1903–36, and from 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94.

Following Efron and Tibshirani (1985) and Manly (1991), the median values and 90% confidence intervals derived from the 100 sets of bootstrapped parameters were used as the parameter estimates and their associated uncertainties. The 100 bootstrap runs were considered sufficient for the LMSE method in this study because a preliminary analysis indicated that differences in the distributions of estimated parameters derived from 100 and 2000 bootstrap runs were small.

Since K_{II} was assumed to be the same as K_I, there were three parameters, r_{II}, q_{II}, and B_{69-70}, to be estimated in modelling CPUE and catch data observed in period II. Although CPUE for period II was derived from accurate records of catch and effort associated with part of the commercial fishery, under-reporting of total catch occurred to a significant extent during period II (Montgomery and Chen, 1996). The extent of under-reporting in different fishing seasons was estimated on the basis of a survey of fishermen (Table 1; Montgomery[1]; Montgomery, unpubl. data). Thus, catch in fishing year j was adjusted from the reported catch (Fig. 1) as

$$(Adjusted\,catch)_j = \frac{(reported\,catch)_j}{1-(adjustment\,coefficient)_j},$$

where adjustment coefficient = the proportion of under-reporting estimated.

The seven-step procedure described above was modified to include the uncertainties in K_I in estimating the parameters and associated uncertainties in period II. The modification was accomplished by using values of K_I randomly sampled from the bootstrapped samples generated in the bootstrapped LMSE analysis for period I. Such a modification takes into consideration the variation in K_I (thus K_{II}) when estimating q_{II}, r_{II}, and $B_{1969-70}$ and their variabilities.

Table 1

Coefficients used to adjust reported catch data in the period of 1969–70 to 1993–94.

Year	Adjustment coefficient
1969–70 to 1979–80	0.5
1980–81 to 1989–90	0.7
1990–91 to 1991–92	0.45
1992–93 to 1993–94	0.15

Evaluation of probability of overexploitation for next fishing season

The probability of short-term overexploitation (i.e. the probability of the fishing mortality rate being higher than defined biological reference points) was defined with respect to different levels of catch for the 1996–97 fishing season. The two biological reference points used in our study were $f_{0.1}$ and f_{MSY}. The $f_{0.1}$ is equivalent to the more commonly used $F_{0.1}$ (Hilborn and Walters, 1992) and is defined by the equation

$$\left.\frac{\partial C(E)}{\partial E}\right|_{E=f_{0.1}q} = 0.1\left.\frac{\partial C(E)}{\partial E}\right|_{E=0},$$

where $C(E)$ = the equilibrium yield corresponding to effort E (Punt, 1993).

From the above equation and Equation 1, $f_{0.1}$ can be calculated as $f_{0.1} = 0.45r$. The TAC in year j based on the $f_{0.1}$ can be calculated as $TAC_{0.1}(j) = 0.45rB_j$, where B_j is the estimate of stock biomass in year j. The rate of fishing mortality (f_{MSY}) producing maximum sustainable yield (MSY) can be calculated as $f_{MSY} = 0.5r$. The TAC in year j, based on f_{MSY}, can be calculated as $TAC_{MSY}(j) = 0.5rB_j$. It should be noted that the $TAC_{MSY}(j)$ calculated above changes with the current stock biomass and is thus dynamic over time. It differs from the commonly used equilibrium maximum sustainable yield (EMSY) calculated as $rK/4$ (Hilborn and Walters, 1992). The use of $TAC_{MSY}(j)$ is more robust with respect to interannual variability in the biomass of the stock than is a TAC based on the more commonly used EMSY.

Results

Parameters r_I, q_I, and K_I estimated with the LMSE method were 0.203, 1.76×10^{-6} (per vessel, and 3208 t, respectively. This results in an EMSY of 163 t. The predicted CPUEs tended to follow the CPUEs observed in the majority of years in period I (Fig. 2). However, CPUEs observed in the years 1904 and 1917–24 differed considerably from the LMSE-predicted values, indicating that they virtually were ignored in the parameter estimation. The estimated stock size in year 1936 was 37.6% of the virgin biomass. The median value for K_I from the 100 bootstrapped LMSE estimates was 4084 t (Table 2), about 27% higher than the LMSE-estimated K_I. The coefficient of variation (CV) for the LMSE-estimated K_I was only 26%, indicating that the uncertainty associated with the LMSE-estimated K_I was small. The median values of bootstrapped r and q were 0.155 and 1.2×10^{-6} (per vessel) (Table 2), about 24% and 32% lower than the LMSE-estimated r and q, respectively. The higher CV for r, compared with the CVs for q and K_I, indicates that the estimate of r is more uncertain than the estimates of q and K_I. The distributions of all three parameters tended to be positively skewed (Fig. 3). The estimated EMSY ranged from 50 t to 200 t with the median value of 151 t (Fig. 3).

By assuming K_{II} to be the same as the median value of K_I estimated in the bootstrapped LMSE estimation, we estimated parameters r_{II}, q_{II}, and $B_{1969-70}$. The LMSE-estimated $B_{1969-70}$ was close to the value of K_I (4,365 t). The r_{II} was 0.218, about 7% higher than the LMSE-estimated r_I. The LMSE-estimated q_{II} was 0.15 $\times 10^{-6}$ (per trap-month). The model was fitted by means of the LMSE method by ignoring the data observed in the two fishing seasons 1971–72 and 1974–75 because

Table 2

Summary of the estimates of parameters with the bootstrapped LMSE method from 100 runs of bootstrap simulation for CPUE and catch data observed during 1903 to 1936.

	Parameter			
Statistic	r_I	$q_I \times 10^{-6}$ (per vessel)	K_I	σ^1
Median	0.155	1.20	4084	0.428
Mean	0.149	1.26	4269	0.497
CV	48.6%	28.0%	26.0%	53.1%
5th%	0.045	0.79	2554	0.187
95th%	0.292	1.94	6400	1.058

[1] For each bootstrap run, σ is calculated as

$$\sigma = \sqrt{\frac{\sum_{1}^{n}(CPUE - \overline{CPUE})^2}{n}},$$

where CPUE and $\overline{CPUE}$ are observed and predicted catch per unit of effort, respectively, and n is the number of years.

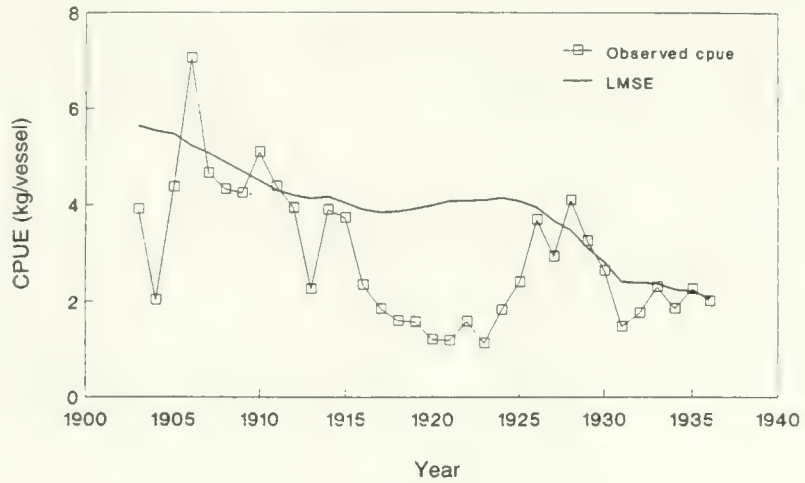

Figure 2

Catch per unit of effort observed and predicted by the LMSE method for the NSW eastern rock lobster fishery in the period of 1903 to 1936.

CPUEs in these two fishing seasons increased greatly and abruptly from the previous years, followed by an equally abrupt decrease (Fig. 4).

Distributions for parameters of the model estimated with the bootstrapped LMSE method for period II are presented in Figure 5. The median value of the stock biomass in year 1969–70 was 3808 t, 13% lower than the corresponding LMSE estimate. The estimated median value of r_{II} was 0.172 (Table 3), 22% lower than the LMSE-estimated r_{II}. The median value of q_{II} was only 10% of that estimated for q_I. This resulted from different units of fishing efforts used in calculating the abundance index (CPUE) in the two

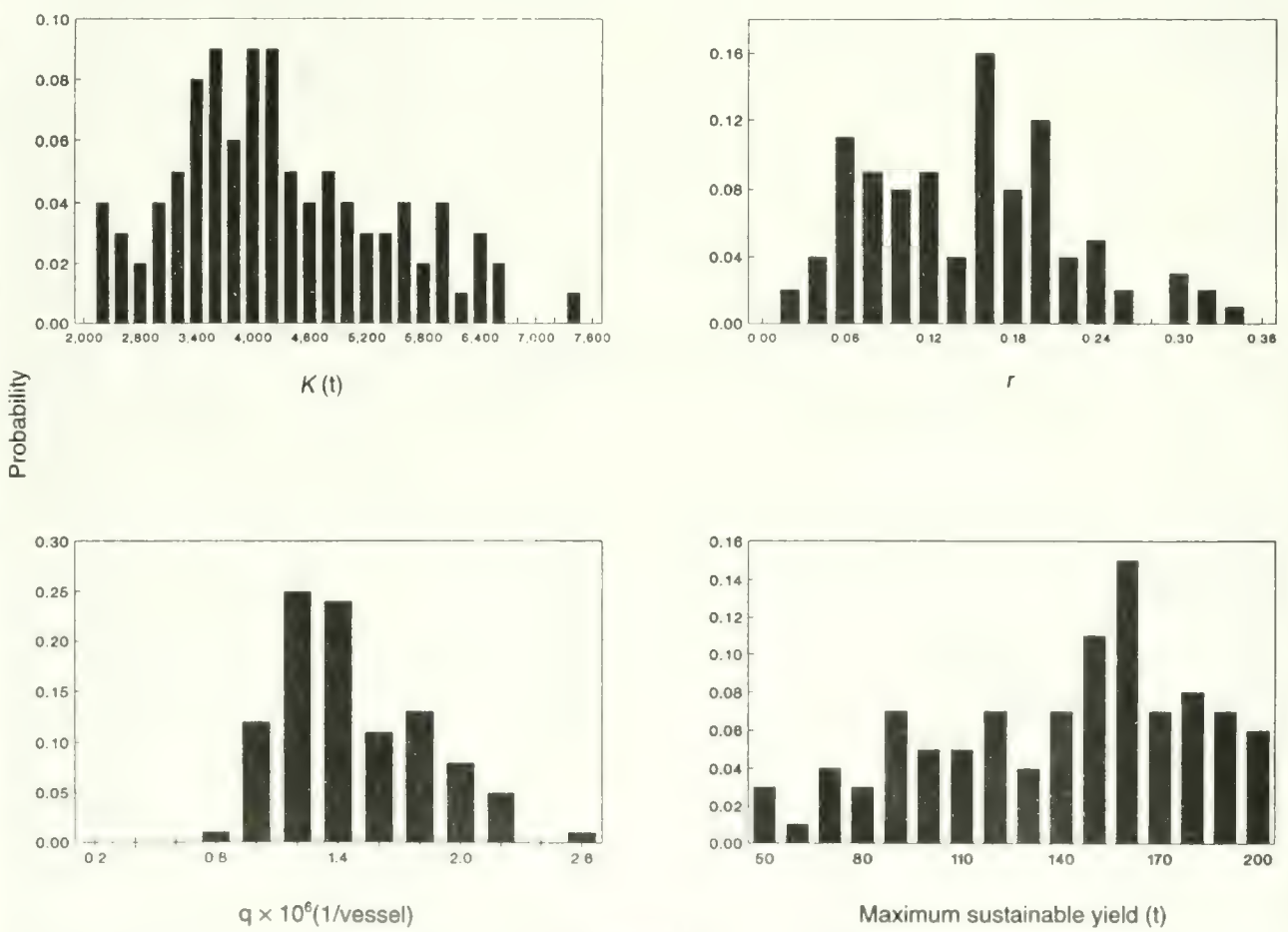

Figure 3

The distributions of the parameters estimated with the bootstrapped least median of squared errors (LMSE) for the period of 1903 to 1936.

time periods (per vessel versus per trap-month). The CVs and 90% confidence intervals for the parameters were small (Table 3), indicating that estimates of parameters for period II had small uncertainties. The estimated EMSY ranged from 80 t to over 200 t with a median value of 120 t (Fig. 5).

The median and 5th and 95th percentiles of the biomass of the stock for each year in period II are plotted in Figure 6. The calculation of total catches for 1994–95 and 1995–96 had not been completed when this study was conducted. However, the TAC of 106 t was likely to have been fully realized in each of these years. Thus, the biomasses of the stock for 1995–96 and 1996–97 were projected based upon the assumption that catches in 1994–95 and 1995–96 were 106 t. The 90% confidence intervals tended to increase from 1969–70 to 1994–95 (Fig. 6), indicating that estimates of the stock biomass in recent years were less precise than those in earlier years. The median value of the biomass of stock in the 1995–96 fishing year was 1420 t, and the 5th and 95th percentiles were 710 and 2719 t (Fig. 6). Median values for the biomass of the stock fell until 1990–91 and then started to increase from 1992–93. The plot of the distribution of the ratio between biomass in year 1995–96 against the biomass of the virgin stock indicated that there was more than 75% chance that the biomass ranged between 15% and 30% of the virgin biomass (Fig. 7).

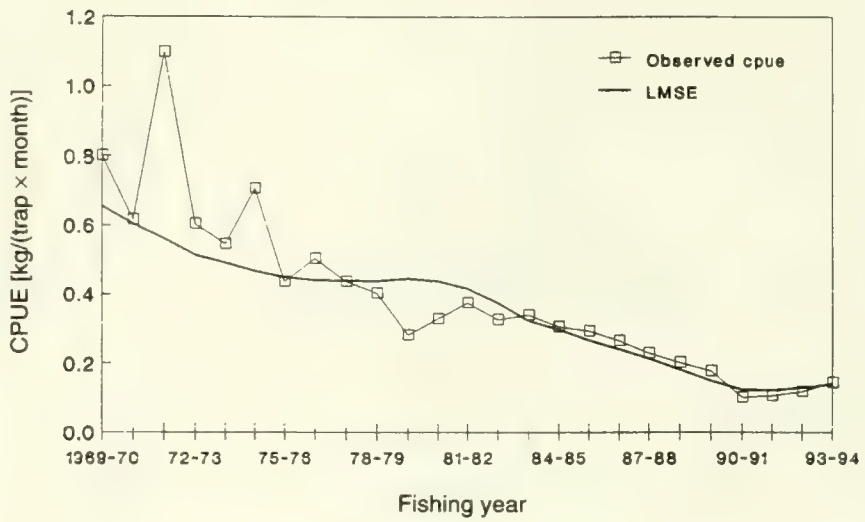

Figure 4

Catch per unit of effort observed and predicted with the LMSE method for the NSW eastern rock lobster fishery during the period of 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94 (i.e. 1 July 1993 to 30 June 1994).

Table 3

Summary of the estimates of parameters using the LMSE method from 100 runs of bootstrap simulation for CPUE and catch data observed from 1969–70 to 1993–94.

	Parameter			
Statistic	r_{II}	$q_{II} \times 10^{-6}$ (trap × month)$^{-1}$	$B_{1969\text{-}70}$ (ton)	σ^1
Median	0.172	0.15	3808	0.237
Mean	0.177	0.15	3764	0.241
CV	19.4%	16.2%	11.5%	360%
5th%	0.132	0.11	3099	0.059
95th%	0.223	0.18	4418	1.098

[1] For each bootstrap run, σ is calculated as

$$\sigma = \sqrt{\frac{\sum_{j=1}^{n}(CPUE_j - \hat{CPUE}_j)^2}{n}},$$

where CPUE and $\hat{CPUE}$ are observed and predicted catch per unit of effort, respectively, and n is the number of years.

The distribution of the biomass of the stock in 1996–97 is summarized in Figure 8. There was more than a 70% chance that the biomass of the stock ranged between 1000 to 1750 t. The probabilities of short-term overharvest (i.e. exceeding the selected biological reference points) were calculated for different levels of catch in 1996–97 on the basis of the distribution estimated for the biomass of the stock in 1996–97 (Fig. 9). For example, the TAC of 100 t would have a 30% chance of exceeding the reference point f_{MSY}, and a 40% chance of exceeding $f_{0.1}$ (Fig. 9).

Discussion

The model used in this study is one of the simplest models commonly used in fish stock assessment (Hilborn and Walters, 1992). An essential assumption of this model, as with similar models, is that the relationship between CPUE and the biomass of the stock remains constant over time. Because of the use of the robust estimator, this assumption becomes the following: the proportional relationship between the

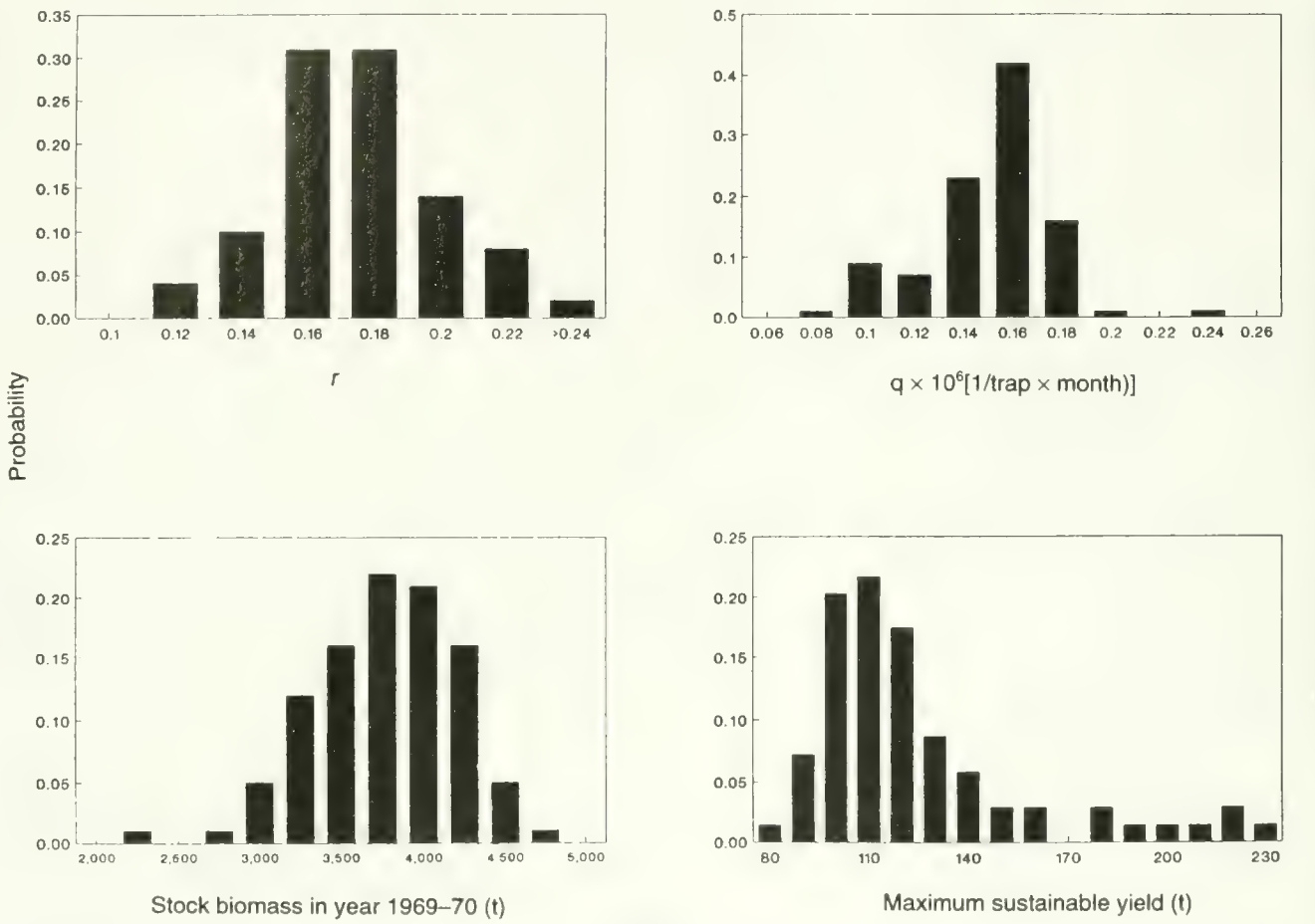

Figure 5

The distributions of the parameters estimated with the bootstrapped least median of squared errors (LMSE) for the period of 1969–70 to 1993–94.

stock biomass and CPUE is the same for the majority of years.

Compared with traditional least-squares estimation methods, the LMSE method tends to fit the model to the majority of the data, and its estimates of parameters are not affected by atypical data observed in a few years (Chen et al., 1994). Thus, if atypical observations arise, parameter estimation with the LMSE will not be affected greatly. Because the LMSE is not sensitive to atypical data, these data tend to be far from the LMSE-estimated CPUEs (Figs. 2 and 3) and thus are readily detected. However, it is important to determine why an observed CPUE is far from the predicted CPUE. Such a practice requires extensive background information on the fishery. Apart from exceptionally large observation errors, atypical observations may arise from unusual environmental conditions and substantial changes in fishing methods and locations. The nature of atypical observations resulting from unusual environmental conditions differs from those resulting from unusual observation errors. These atypical data should be considered separately from those observed under normal conditions in the stock assessment process because such unusual conditions last only for a short period of time in the development of the fishery (Chen et al., 1994). For example, the observed CPUE in 1971–72 was much higher than the LMSE-estimated CPUE (Fig. 4). This might result from the fishery being expanded in that year to include aggregations of lobsters on the previously unexploited slopes of the continental shelf. This would result in a high q for that year. Clearly, such a high level of CPUE cannot be sustained for long and should not be interpreted as an indicator of large stock biomass for that year. CPUEs observed from years 1917 to 1924 were much lower than the LMSE predicted (Fig. 2). This finding may be related to large observation errors in CPUEs. For this period, the number of fishing boats (other than trawlers or Dan-

ish seiners) that operated from lobster producing ports and in oceanic waters was used as an index of fishing effort for the lobster fishery. This was done because it was impossible to distinguish between vessels that were used for fishing lobsters and vessels that were used for fishing other species in the same area (Montgomery, 1995). During this period, annual landings of lobsters were probably under-reported because only lobsters sold at the main market centers were recorded. Such an over-estimation of efforts and under-estimation of catches would lead to under-estimation of CPUE for this period of time. It should be realized, however, that the above reasons for the large deviation of observed data from model estimates remain a working hypothesis.

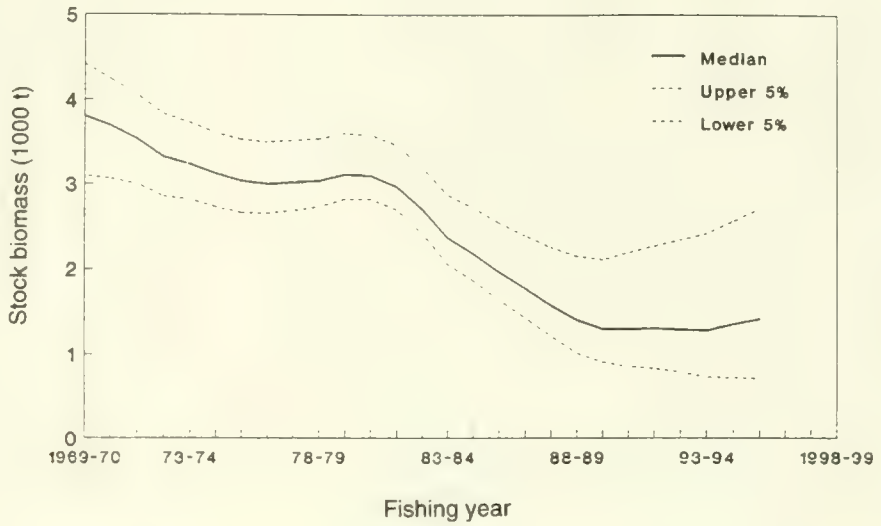

Figure 6

The median and 90% confidence intervals of stock biomass predicted with the bootstrapped LMSE method for the period of 1969–70 to 1995–96.

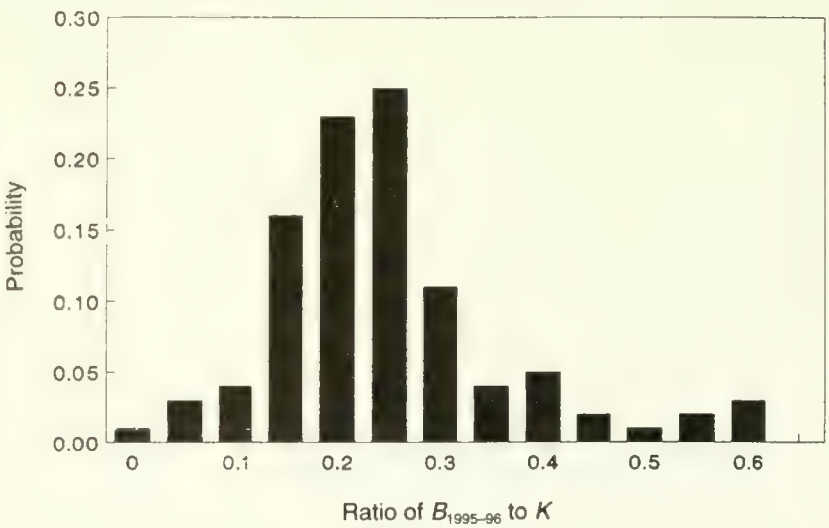

Figure 7

The distribution of the ratio between the biomass of the stock in 1995–96 ($B_{1995-96}$) and the biomass of the virgin stock (K) estimated with the bootstrapped LMSE method.

Outliers can be identified in linear regression analyses by using criteria developed by Rousseeuw and Leroy (1987). However, the criteria developed through extensive simulations based on a linear regression model cannot be used in nonlinear regression analysis. An extensive simulation study is needed to develop suitable criteria to identify outliers in nonlinear regression analyses. Before this can be done, the LMSE-based reweighted least squares, which has been shown to behave better than the least median of squares in linear regression analyses (Chen et al., 1994; Chen and Paloheimo, 1995), cannot be used in nonlinear regression analyses.

The results presented in our paper were based on catch data adjusted by using one set of adjustment coefficients. To test the sensitivity of the results to the adjustment coefficients, we also used two other sets of adjustment coefficients in the analysis (Table 4). These two sets of coefficients have more extreme values than the one presented in Table 1. The detailed results for these two sets of data were reported in Montgomery and Chen (1996). We plotted the stock biomass estimated with these three sets of data (Fig. 10). Although there are differences, they are rather small considering the large differences in adjustment coefficients. This may indicate that the results presented in this paper tend not to be sensitive to small changes in catch adjustment coefficients used in period II.

It is clear that the size of the lobster stock off New South Wales was low, with respect to its virgin biomass, as was the 75% confidence. Recent stock biomass (i.e. in 1995–96) has been between 15% and slightly over 30% of the virgin biomass. However, it seems that the decline in the biomass of the stock has stopped in recent years, and that the stock is perhaps in a period of recovery.

Data observed in the two periods of time were modeled separately in our study. An alternative, perhaps better approach is to combine these two time periods with information on catches landed within the intervening period. This approach will be used in the next stock assessment when good estimates of catches from 1939 to 1968–69 become available.

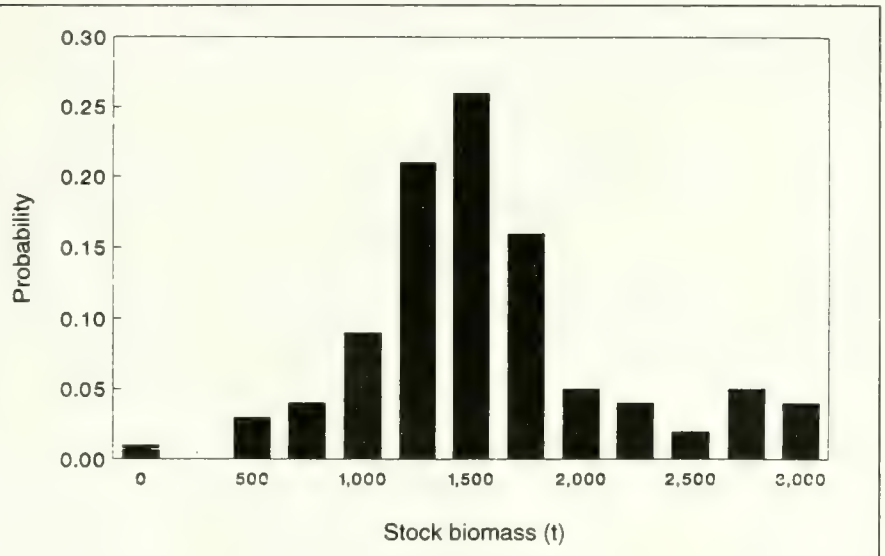

Figure 8

The distribution of stock biomass in 1996–97 estimated with the bootstrapped LMSE method.

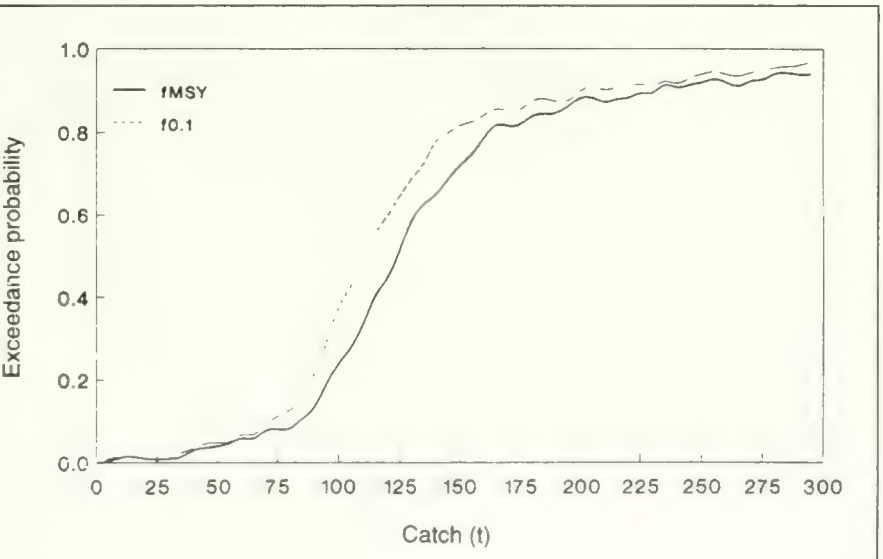

Figure 9

Probability of short-term overharvest (i.e. exceeding the selected reference points $f_{0.1}$ and f_{MSY}) for fishing year 1996–97.

Because the data were limited, the choice of models that can be used to describe the dynamics of lobster stock in NSW is also limited. Two disadvantages of using the simple production models are 1) an inadequate representation of the fishery dynamics may result in large biases in estimates of parameters and biomasses, and 2) extra assumptions are needed about fisheries (e.g. CPUE is a good indicator of stock abundance). However, these simple models also have their advantages. If the model fails, this failure can be seen easily. Because of the simple mathematical structure and lack of constraints in the parameter estimation, estimates of parameters may not necessarily be biologically reasonable (e.g. as negative values), an indication of the failure of models or data (Hilborn and Walters, 1992). It is now fashionable to mimic biological and fisheries realism by setting up a model that is mathematically and statistically complicated. Although advantages are obvious, disadvantages associated with this type of models may not always be realized. In addition to the requirement of extra input data, such models tend to have some undesirable attributes in the estimation of parameters, such as overfitting and high correlations among estimates of parameters. Incorporation of different biological and fisheries processes (e.g. fishing and recruitment processes) into one model for parameter estimation can also create some

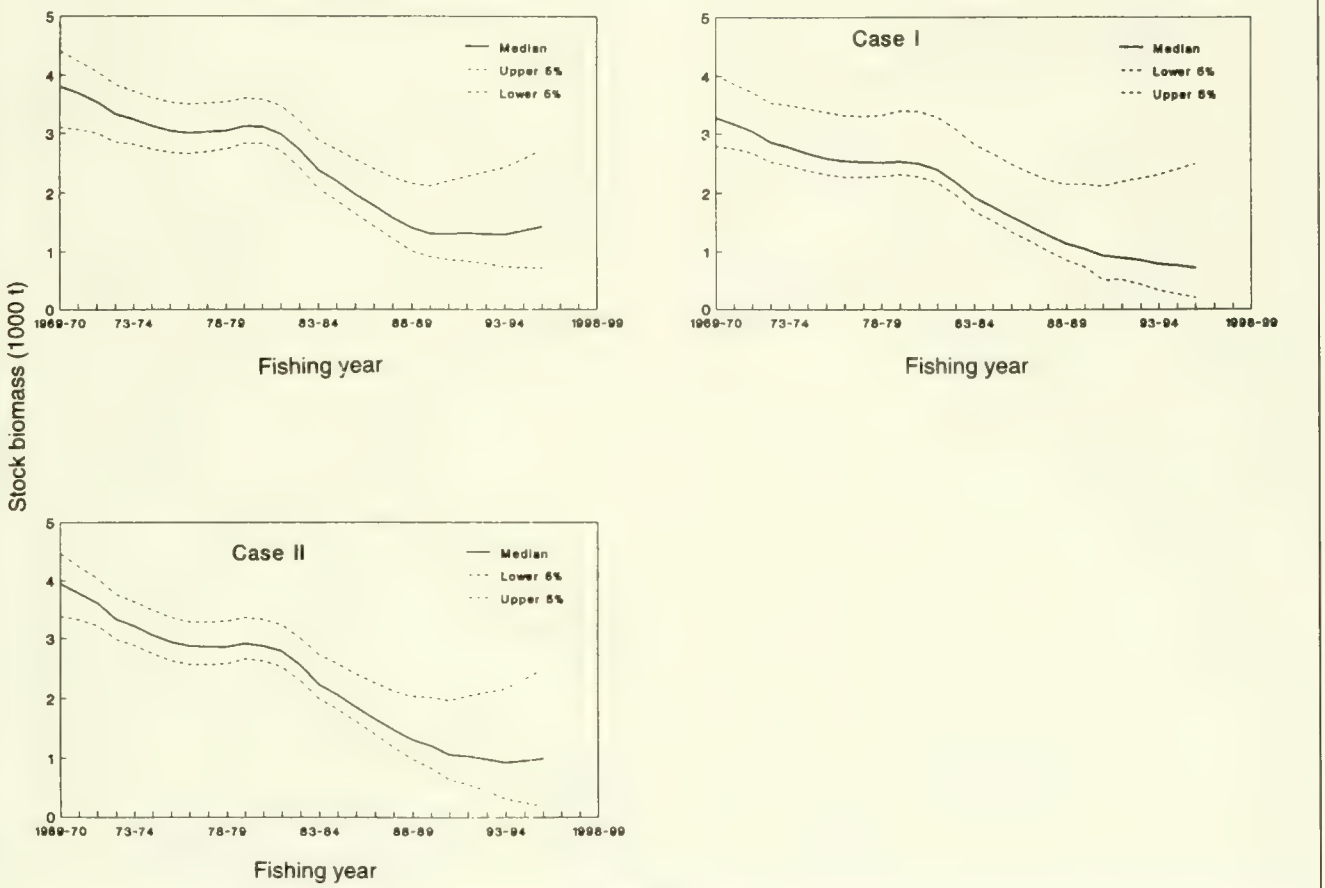

Figure 10

The predicted median and 90% confidence intervals of stock biomass for three sets of adjustment coefficients for the period of 1969–70 to 1995–96.

artificial links among parameters (e.g. between catchability coefficient and recruitment). A large number of built-in constraints (e.g. parameter A must have a value between A_1 and A_2) are often required to facilitate parameter estimation for such a model. This may artificially result in parameters having biologically reasonable estimates, even if the model fails. Such a feature also encourages the indiscriminate and uncritical use of stock assessment models, which leads to the misinterpretation of results. The extra biological or fisheries information (e.g. size structure, recruitment and spatial distribution) often incorporated into a dynamic model will certainly increase the accuracy and reliability in the estimation of parameters if the information is accurate. However, in practice, extra information is likely to be subject to large errors. In this case, a complicated model assimilating extra information will probably fail because its validation requires that each piece of information be true (Xiao[2]).

It is well known that the current biomass for a decreasing stock is often over-estimated when production models are used in assessment with the least squares method (e.g. Schnute, 1989; Hilborn and

Table 4

Coefficients used to test the sensitivity of the stock assessment to adjustment coefficients used to adjust reported catch data in the period from 1969–70 to 1993–94.

	Adjustment coefficient	
Year	Case I	Case II
1969–70 to 1979–80	0.4	0.6
1980–81 to 1989–90	0.6	0.7
1990–91 to 1991–92	0.3	0.5
1992–93 to 1993–94	0.1	0.2

[2] Xiao, Y. 1997. A theoretical consideration of subtleties in, and problems with, use of production models. Commonwealth Scientific and Industrial Research Organization (CSIRO) Marine Laboratory, Hobart, Australia. Unpubl. manuscript.

Walters, 1992; Polacheck et al., 1993; Chen and Andrew, 1998). In our study, when the maximum likelihood (ML) method was used, the r_I, q_I, and K_I had values of 0.041, 0.40×10^{-6} (per vessel), and 8,667 t, respectively. These are 20%, 23%, and 270% of the LMSE-estimated parameters, and 26%, 33%, and 213% of the median values of the bootstrapped LMSE estimates. According to the ML method, the eastern rock lobster stock had a large biomass with a low productivity rate. In contrast, the LMSE method predicted a smaller stock with a relatively high productivity rate. This difference arises from different methods used to fit the model to CPUE data. The ML was heavily influenced by the CPUEs observed from 1916 through 1924, whereas the LMSE virtually ignored these observations and tended to follow closely the CPUE in the majority of years (Fig. 11). Because of the high likelihood of under-estimation of CPUEs from 1916 through 1924, the LMSE method is probably more suitable. The estimates of r_{II}, q_{II}, and $B_{1969-70}$ by the ML method were 0.17, 0.13×10^{-6} (per trap-month) and 7174 t, differing from those estimated with the LMSE and bootstrapped LMSE methods (Table 3). This difference may result from different weightings of data for years 1971–72 and 1974–75. Fitting the model with the LMSE method virtually ignored the data observed in these years, which had much higher CPUEs than other years. However, fitting with the ML method was heavily influenced by these two years of high CPUEs (Fig. 11). Because of the patchy distribution of lobsters in their habitat and the expansion of fishing grounds out to the continental slope off the NSW coast during the early 1970s, it is very likely that these two years of exceptionally high CPUEs resulted from high fishing efficiency (i.e. high q values), which should not be taken as an indicator of high biomass.

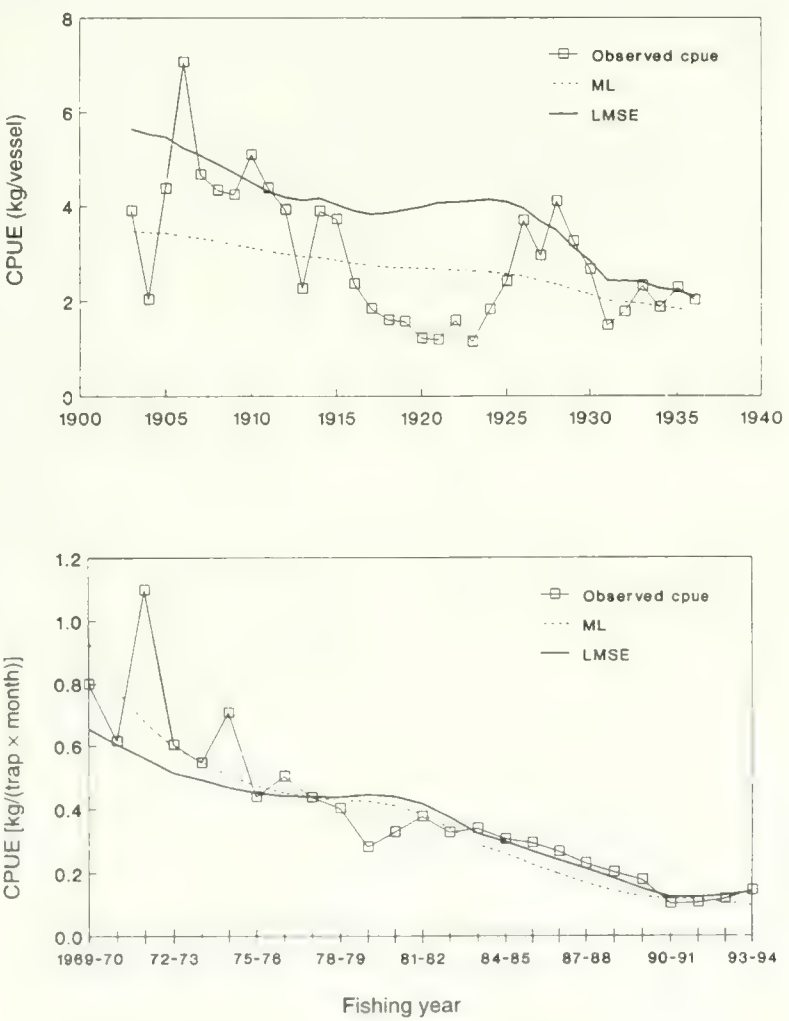

Figure 11

The predicted catch per unit of effort with the maximum likelihood (ML) and least median of squared errors (LMSE) methods for the period of 1903 to 1936 and the period of 1969–70 to 1993–94.

We suggest using the bootstrapped LMSE method as an alternative approach to fitting production models to catch-effort data. The results derived from such an analysis should be evaluated carefully with respect to the biology and ecology of the targeted fish species and with respect to how the catch-effort data were collected. Such an evaluation may shed some light on why some observations differ from the majority which the LMSE estimated line tends to follow. A comparison of results between robust and traditional least squares approaches may lead to a better understanding of the dynamics of the studied fish stock and identification of years in which atypical data are observed.

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Abstract.—The fourbeard rockling, *Enchelyopus cimbrius*, is a small gadid fish found primarily over mud bottoms along the continental margins of the North Atlantic. This study defines the age classes of the fourbeard rockling from the Gulf of Maine, analyzes stomach contents, and characterizes the fish's metazoan parasite fauna. Age was determined from sectioned sagittal otoliths. Nine age classes were identified and compared with the Fraser-Lee back-calculation method. The rate of linear growth was constant throughout age classes. The diet of fourbeard rockling consisted primarily of bivalves, copepods, and decapods, in both number and frequency of occurrence indices. Prey composition in the diet changed with age. One-year-old fish preyed primarily upon copepods; bivalves were second in importance. The reverse was seen in 2–7 year old fish. Data on food habits suggest that the fourbeard rockling is a "grazer." Parasites of this species were one larval nematode, from the family Raphidascaridinae, one larval cestode, *Grillotia erinaceus*, and the two species of adult digenetic trematodes, *Genolinea laticauda* and *Gonocerca phycidis*. Prevalence and abundance data indicate that the parasitic fauna was dominated by Raphidascaridinae sp. and *G. erinaceus*.

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Age and growth, dietary habits, and parasitism of the fourbeard rockling, *Enchelyopus cimbrius*, from the Gulf of Maine

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The fourbeard rockling, *Enchelyopus cimbrius* L., is a small gadid fish found primarily over soft mud or sand bottoms along the continental margins of the North Atlantic Ocean (Bigelow and Schroeder, 1953). This fish lives in burrows during daylight hours and forage at night (Keats and Steele, 1990). Although larval stages of *E. cimbrius* are well documented throughout its range (Battle, 1929; Demir et al., 1985), limited information exists about the age and growth of this species. This study estimates growth rates of *E. cimbrius* from the Gulf of Maine, analyses stomach contents, and characterizes the metazoan parasitic fauna.

Dietary studies for this species have been made at various localities in the eastern North Atlantic (Nagabhushanam, 1965; Wheeler, 1969; Mattson, 1981; Moller-Buchner et al., 1984; Tully and O Ceidigh, 1989), but little is known of the food habits for the western Atlantic, and there have been no dietary reports for *E. cimbrius* from the Gulf of Maine. Diets of *E. cimbrius* vary with location but have been found to consist primarily of polychaetes or crustaceans (Tyler, 1972; Langton and Bowman, 1980; Keats and Steele, 1990).

Records of parasitism of *E. cimbrius* are all apparently coincidental with parasite surveys. Reported parasites include a protozoan (Lom and Laird, 1969), a coccidian (Odense and Logan, 1976), an acanthocephalan (Linton, 1899), digenetic trematodes (Linton, 1899; Gibson and Bray, 1984; Brinkmann, 1988), and a nematode (Nagabhushanam, 1965). No survey of parasites to date has been specifically devoted to this host species.

Materials and methods

A collection of 727 fourbeard rocklings was obtained during the Gulf of Maine Northern Shrimp Survey GM 93-20, 2–13 August 1993. Collections were made during daylight hours at 41 randomly generated stations at depths ranging from 79 to 254 m aboard the NOAA RV *Gloria Michelle* equipped with a 4-seam modified commercial shrimp trawl with a 35-mm stretched mesh. In case of large hauls, a 1-kg random subsample was taken. An additional 36 fish, for stomach analyses, were collected from 6 stations at depths of 170–227 m during the GM 94-12 survey between 2 August and 3 August 1994 by using identical gear and methods.

Specimens collected during the GM 93-20 survey were frozen immediately at sea. To assess the effects of freezing on shrinkage, 218 fresh specimens were individually tagged, measured to the nearest mm for total length (TL), frozen, then remeasured after being thawed for 24 h. Fish were then weighed to the nearest g on a top loading balance and sexed. In addition, both

sagittal otoliths were extracted for ageing purposes and stored dry in coin envelopes.

Fish age classes were determined by counting presumed annual growth increments in otolith sections. For temperate-water fish, which generally exhibit seasonal growth patterns, one year of growth is defined by one opaque and one hyaline zone termed the "annulus" (Pentilla et al., 1988). Sagittal otoliths have been used for age determination in the majority of commercially important gadids (Andrade and Smith, 1988; Dery 1988; Pentilla, 1988) including *E. cimbrius* (Cohen et al, 1990). The assumption that increments were annual in *E. cimbrius* was based on the following: prolonged spawning in the Gulf of Maine (May–October) (Cohen et al, 1990), a pelagic stage (40.0–45.0 mm TL) spanning several months (Bigelow and Schroeder, 1953), time of year sample was taken (August), and presence of a prominent hyaline zone. The otolith of the smallest fish (95 mm TL) in the present study exhibits a prominent hyaline zone and this fish is assumed to have hatched in the previous year.

One otolith from each pair was embedded in a mixture of 1 part carbon powder and 4 parts paraffin wax, then sectioned dorsoventrally through the nucleus on an Isomet saw producing a section 203 µm thick. Sections were mounted on glass slides with Crystal Bond 509, polished with 3.0-µ and 0.5-µ metallurgic lapping film, etched for 6 minutes with 5% EDTA, and stained for 3 minutes with 0.1% toluidine blue. Otolith sections were viewed under a compound microscope at 40× by using transmitted light (Fig. 1). Etching with EDTA provided three-dimensional relief to the polished otolith surface, affording the greatest resolution and definition of the hyaline zones (Secor et al., 1992).

To reduce sample size for age determinations, the length-frequency distribution of *E. cimbrius* at station 40 was used to generate a rarefaction curve. Fifty-seven fish were aged by using both left and right sagittal otoliths during one trial under the following treatment effects: low-power dissecting microscope (LD); high-power zoom stereomicroscope (HS); and high-power zoom stereomicroscope after otoliths were etched with EDTA and stained with toluidine blue (EDTA). Nine fish were omitted from the analysis because of the inability to obtain either the left or the right otolith.

Individual variances of the six trials were plotted in groups of five to generate a rarefaction curve. The

Figure 1

Transverse section of a sagittal otolith etched with 5% EDTA and stained with 0.01% toluidine blue photographed under a compound microscope at 40× by using transmitted light.

magnitude of the variance was stabilized at 30 fish per age class, yielding approximately 270 specimens to be aged. A length-based stratification was developed to avoid underrepresentation of the least abundant fish located at the extremes (Fournier, 1983). After removing the 77 lower (95–129 mm TL) and 54 upper (250–328 mm TL) extremes, 150 rocklings between 130 and 249 mm TL were randomly selected, then added to the extremes, yielding a total subsample size of 281 fish.

Otoliths from 281 fourbeard rocklings were etched and stained, then aged with a compound microscope at a magnification of 40 by using transmitted light. After three complete trials, an ANOVA was run on the assigned age classes.

Assigned age classes were compared by using the Fraser-Lee back-calculation formula which assumes that the relationship between individual fish length and otolith length is maintained proportionally throughout the back-calculation (Carlander, 1981)

It is defined as

$$L_i = a + OD_i (L_c - a/OR),$$

Where L_i = estimated total length (TL) when otolith has formed annulus i;
a = intercept of the (TL):otolith length (OL) regression determined from the sample;
OD_i = otolith distance from the nucleus to annulus i;
OR = otolith radius measured form the nucleus to the edge of the anterior rostrum; and
L_c = TL at capture.

Lengths at assigned ages were compared to back-calculated lengths at ages by means of correlation analysis. Total length back-calculation measurements were used to construct a length-frequency distribution to further corroborate ages assigned to length classes by otolith analysis. A Kolmogorov-Smirnoff test was used to test for differences between the observed and back-calculated length-frequency distributions.

Specimens from the GM 94-12 survey were labeled according to station, cut lengthwise along the abdomen, and preserved in 10% formalin. Stomachs were removed and their contents, after identification, summarized by using both numerical and frequency of occurrence indices. These analyses were further divided into two length categories: 1-year-old (105–121 mm TL) and 2–7 year old (119–271 mm TL) fish, on the basis of assigned age-class information. The size range of the first year class was calculated by using ±1 standard deviation from the mean. The second category, 2–7 year old fish, was calculated by using the −1 deviation of the mean size of the age-2 year class and the +1 deviation of the age-7 year class. Fish (n=1) that fitted within the size limits of these two age groups were placed in the category with the smallest difference between mean age-class length and length of the fish.

In addition to the 36 stomach samples from the GM 94-12 survey, a sample of 112 frozen fish from the GM 93-20 survey was obtained to inspect for occurrence of parasitism. Each gastrointestinal tract was removed and cut into its component parts, then sliced lengthwise to allow for inspection with a dissecting microscope. Nematodes were labeled according to the location of infection, preserved in 70% ethanol, then transferred to 70% ethanol and 5% glycerine.

Trypanorhynch blastocysts and digenetic trematodes were preserved and stored in 10% buffered formalin. Trypanorhynchs were removed from their blastocysts, transferred to 70% ethanol, and stained overnight in Mayer's paracarmine diluted 1:9 in 70% ethanol. Specimens were destained in 0.1 HCl in 70% ethanol until internal organs were visible, neutralized with 70% sodium bicarbonate for 20 minutes, then dehydrated in a graded ethanol series prior to clearing in methyl salicylate. Digenetic trematodes were similarly prepared. Each specimen was mounted on a glass slide in Canada balsam with slides stored flat until the mounting medium had hardened, when they were viewed under a dissecting scope for identification.

Helminth data were summarized by using prevalence, abundance, and intensity indicies. Prevalence (%P) is defined as the number of infected individuals divided by the number of individuals examined multiplied by 100, abundance (A) as the mean number of parasite species per host examined, and intensity range (I range) as the number of parasite species in each infected host (Margolis et al., 1982). Helminth data were further divided into nine length-class categories with ±1 standard deviation from the mean of each age class. Again, fish (n=3) that fitted within the limits of two age classes were treated in the same manner as in the food habits analysis. Splitting the data into length-class categories provided a better indication of the representative parasites in a respective year class than did dividing the data arbitrarily.

Results

Age and growth

The length-frequency distribution of *E. cimbrius* (n=727) sampled during the GM 93-20 survey ranged

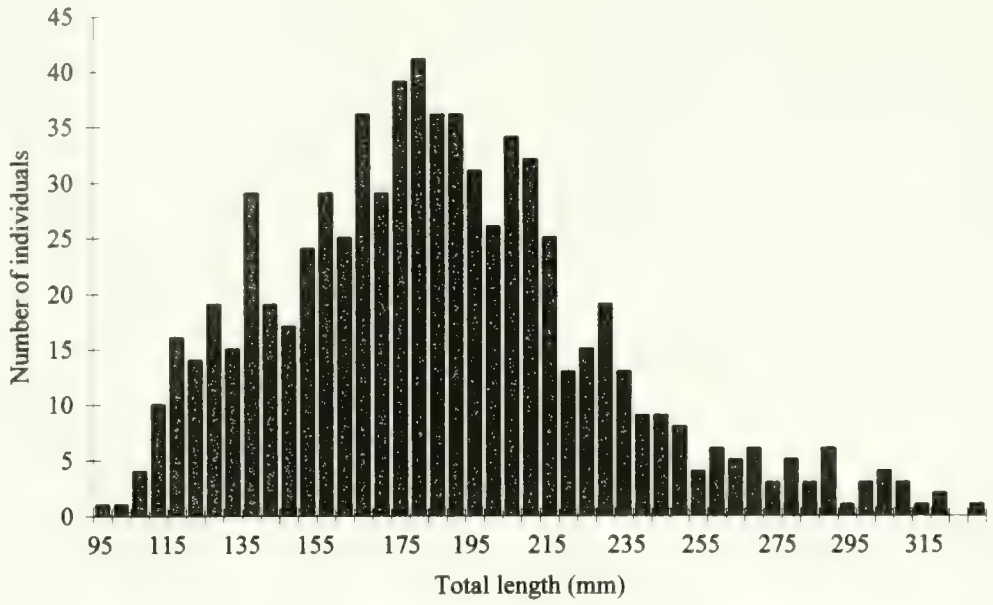


Figure 2

Length-frequency distribution of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5 (e.g. 95=91–95). (n=727).

from 95 to 328 mm TL (Fig. 2). Shrinkage was not significant (P=0.2465), therefore, all total lengths reported in this study are from previously frozen fish.

None of the treatment effects (LD, HS, EDTA) employed on both otoliths from fish collected at station 40 was found to be significantly different (P=0.9488). The EDTA method was selected because it produced the highest r^2 value (r^2=0.9961) in a regression analysis. There was no significant difference between left and right otoliths (P=0.8934).

Nine age classes were identified (Table 1). An ANOVA was run on the assigned ages of the 281 rocklings. The three independent trials were not significantly different from one another (P=0.8028). There was a high correlation (P=0.984) between total length and age (Fig. 3). Because of the difficulty in interpreting annular growth or disagreement about age over the three independent readings, 28 out of 281 otoliths were discarded.

Linear growth was significantly different in males and females (P=0.0001) (Table 2). Nine male and eight female age classes were observed. To account for the sex differences in growth, the length frequency has been subdivided to show the distribution of male, female, and undetermined sexes (Fig. 4). Undetermined sexes were either immature or badly preserved.

There was a significant difference between the weights of males and females (P=0.0001). The average weight of all sexed specimens regardless of age showed that males weighed more than females (mean 26.5 ±19.3 and 24.5 ±24.2 g, respectively). Females were heavier at age than males for the first three year classes (Fig. 5). A scattergram of age versus total length (mm) and weight (g) is presented in Figure 6.

Regression analysis of TL vs. OL is defined by $y = 0.014x + 0.838$ where 0.838 is the intercept used to standardize the Fraser-Lee back-calculation equation. Back-calculated lengths at age (Table 3) and

Table 1

Age-class statistics based on observed otolith readings of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=253).

		Total length (mm)		
Age class	n	Mean	Range	SD
1	37	112.6	95.0–127.0	8.1
2	52	127.4	115.0–149.0	8.5
3	24	157.3	142.0–178.0	8.8
4	38	180.5	155.0–207.0	12.4
5	35	204.3	189.0–226.0	9.2
6	16	240.7	223.0–268.0	13.8
7	26	258.5	228.0–282.0	12.8
8	13	283.6	272.0–297.0	6.8
9	12	307.7	293.0–328.0	9.9

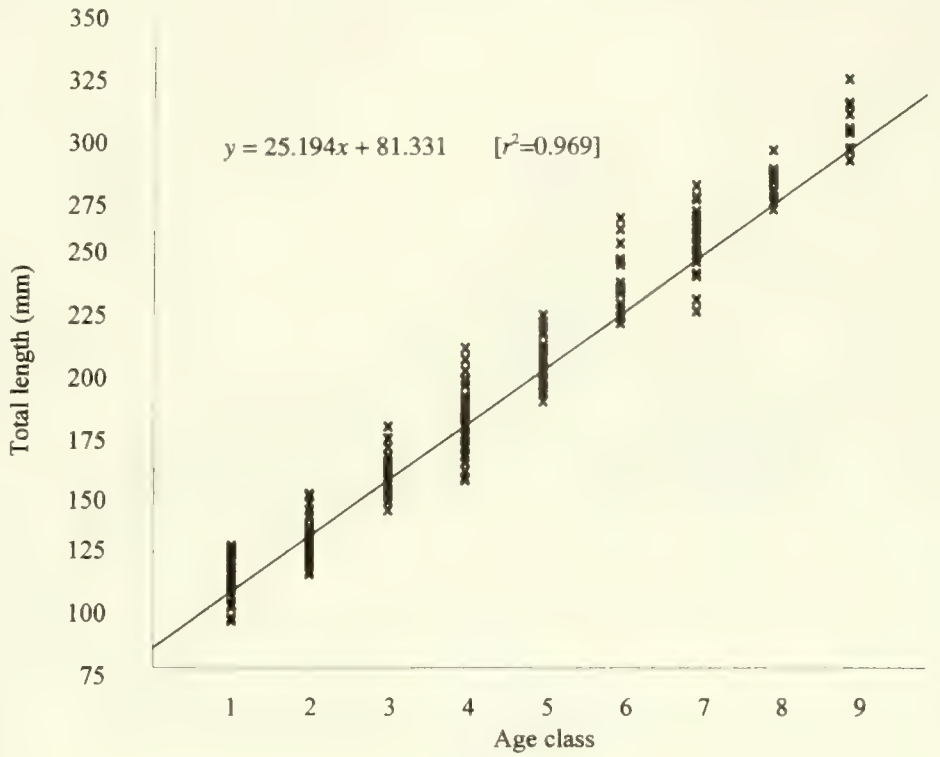


Figure 3

Regression of observed age-class data vs. total length (mm) of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=253).

observed lengths at age were not significantly different (P=0.9608). The Kolmogorov-Smirnoff test revealed there was no significant difference between the back-calculated and observed length-frequency distributions (P=0.3124) (Fig. 7). In addition, back-calculated and observed lengths at ages were highly correlated (P=0.996).

Dietary habits

Stomach contents consisted primarily of mollusks and arthropods. Three specimens contained no food and were not included in the determination of numerical and frequency of occurrence indices. *Yoldia* sp. and calanoid copepods composed the majority of prey items in both number and frequency (Table 4). *Yoldia* sp. and calanoid copepods, combined with *Diastylis quadrispinosa*, *Crangon septemspinosa*, unidentified cumaceans and decapods, composed 91.6% of the prey items ingested. Frequency indices showed that the latter four prey items had similar frequencies.

Numerical indices show that copepods composed 71.2% of the diet of 1-year-old fish (Table 5). Bivalves were second in importance (19.2%), followed by cumaceans (5.4%), amphipods (2.7%), and decapods (1.4%). The importance of copepods decreased to

Table 2

Mean lengths of males, females, and immature or undetermined sexes per age class based on observed otolith readings. (n=253).

		Mean total length (mm)		
Age class	n	Male	Female	Immature or undetermined
1	37	116.7	113.3	110.7
2	52	130.6	125.7	125.8
3	24	158.0	155.8	160.3
4	38	180.0	181.2	—
5	35	204.0	204.5	—
6	16	239.4	242.8	—
7	26	257.9	257.5	277.0
8	13	281.8	287.0	286.0
9	12	307.7	—	—

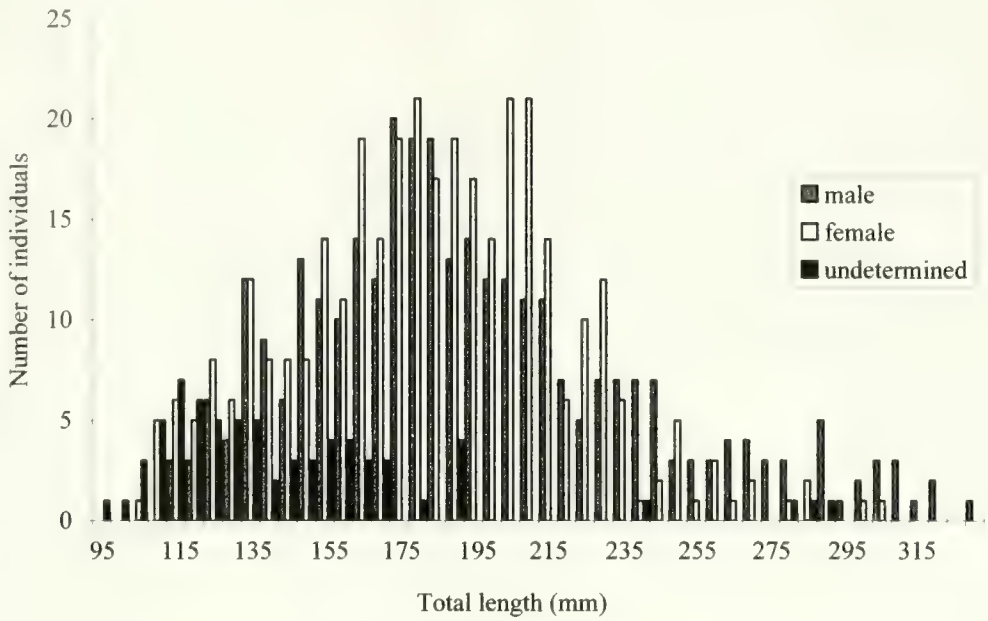


Figure 4

Length-frequency distribution of males, females, and undetermined sexes collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5. (n=727).

28.7% and was replaced by bivalves (56.3%) in fish ranging from 2 to 7 years old (Table 5). Polychaetes (2.0%) and decapods (3.7%) were found only in the stomachs of older fish. Cumaceans made up a small percentage of the diet in both size ranges.

Bivalves (80.0%) and copepods (80.0%) were the most frequent items encountered in 1-year-olds, with cumaceans (40.0%) third in importance (Table 5). The frequency of bivalves (71.0%) in the diet of older fish was similar to that of 1-year-olds. Decapods and polychaetes were consumed in higher frequency in larger fish. Copepods were eaten in large numbers in both size categories but were taken less frequently by larger fish (12.9%).

Parasitism

Four parasite species were identified for the first time for this host. The nematodes were identified as all second- or third-stage and third- or fourth-stage larvae of the family Raphidascarinidae, probably *Hysterothylacium* sp. These identifications were based on the presence of a boring tooth, globular ventriculus, ventricular appendage, intestinal caecum, and excretory pore near the nerve ring. Raphidascarinidae sp., located mainly in the body cavity, were found to have the highest prevalence (23.0%) of all parasites surveyed (Table 6).

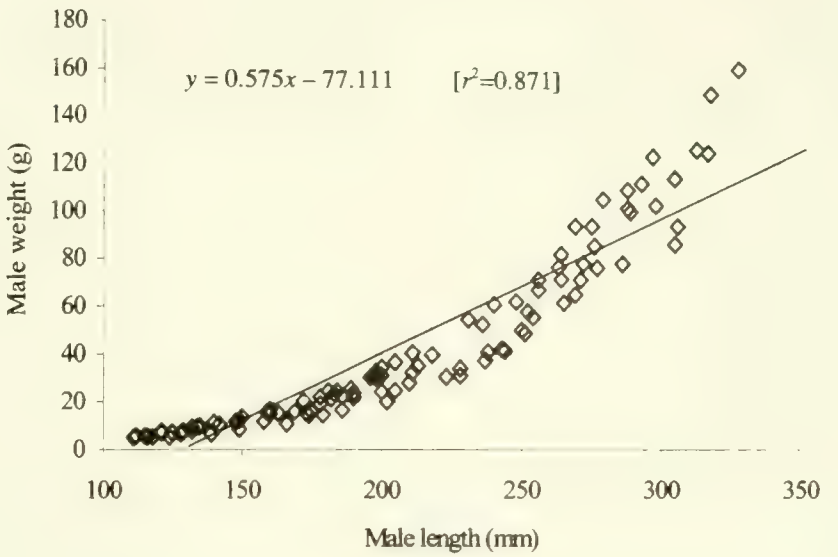
Table 3

Age-class statistics based on back-calculated lengths at age of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=40).

	Total length (mm)		
Age class	Mean	Range	SD
1	102.3	86.0–118.0	8.1
2	127.7	116.0–140.0	6.8
3	153.8	140.0–174.0	8.0
4	183.1	167.0–202.0	9.5
5	212.9	191.0–231.0	10.0
6	235.5	223.0–260.0	9.6
7	257.1	244.0–270.0	8.2
8	280.0	272.0–287.0	6.2

Encysted plerocerci larvae were identified as *Grillotia erinaceus* Van Beneden, 1858 and were found in the body cavity, stomach, and intestine of 20.9% of the fish examined.

The two species of digenetic trematodes, found in the stomachs of *E. cimbrius* collected during the GM 94-12 survey, were identified as *Genolinea laticauda* Manter, 1925 and *Gonocerca phycidis* Manter, 1925. Body length dimensions of two specimens of *G.*



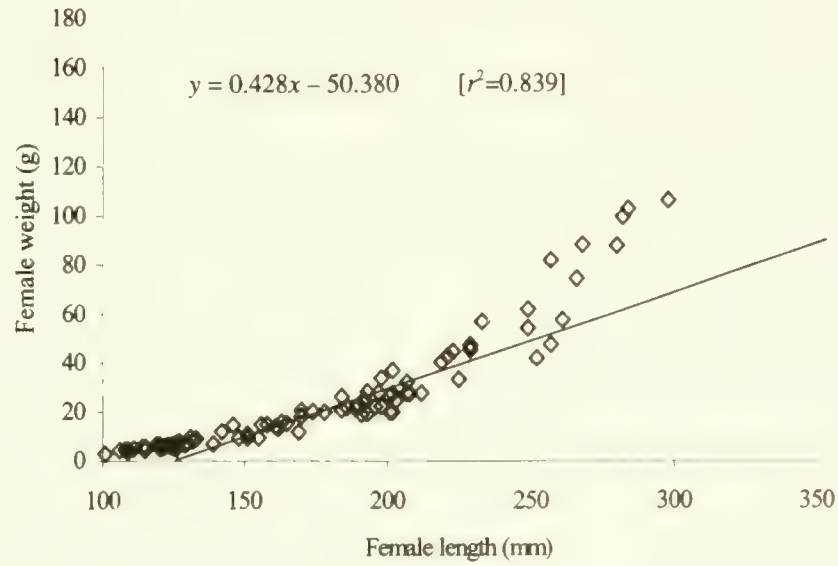


Figure 5

Regression of male length (mm) vs. male weight (g) (n=119) and female length (mm) vs. female weight (g) (n=96) for *E. cimbrius* collected during the GM 93-20 survey.

laticauda and *G. phycidis* ranged from 1.26 to 1.34 mm and from 1.38 to 1.76 mm, respectively. Both digenetic trematodes were found in low prevalence (4.7% and 1.4%, respectively) (Table 6).

The prevalence of infection of Raphidascarinidae sp. steadily increased from 8.3% in 1-year-olds to 100.0% in 9-year-olds (Table 7). The prevalence of *G. erinaceus* fluctuated but generally increased with fish age. There was an increase in infection from 9.1% to 20.0% and 25.0%, respectively by Raphidascarinidae sp. and *G. erinaceus* in 2- and 3-year-old fish. Infection by *G. laticauda* and *G. phycidis* was minimal in all size classes. All helminths in all year classes were found in low abundance.

Discussion

Age and growth

The age distribution of the sample comprised primarily of 3-, 4-, and 5-year-old *E. cimbrius*, with a maximum age of 9. The maximum age attained by this species in the Gulf of Maine is similar to that

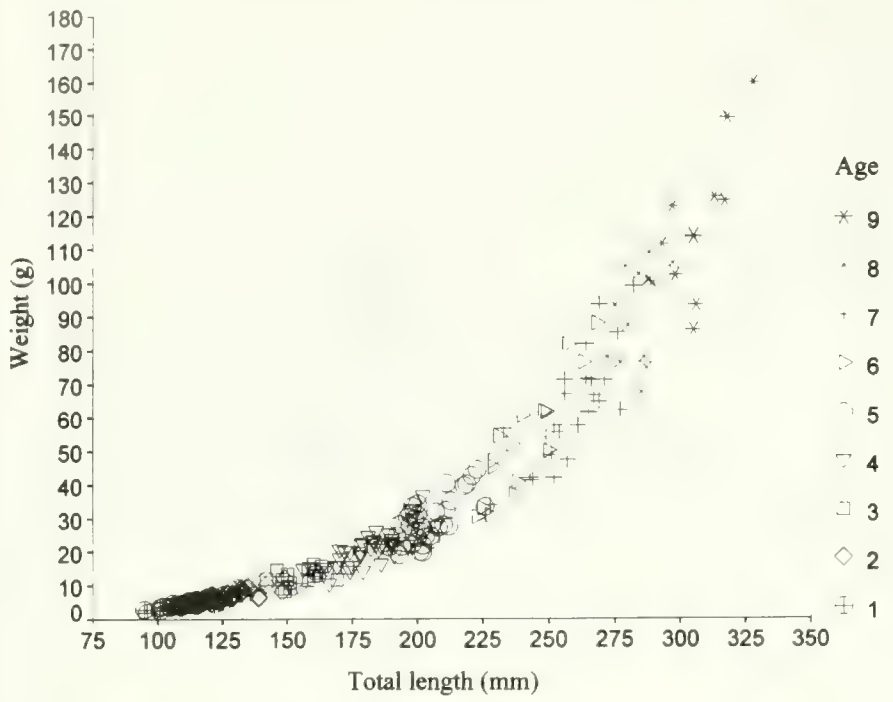


Figure 6

Scattergram of age vs. total length (mm) and weight (g) for *E. cimbrius* collected during the GM 93-20 survey. (n=241).

reported from the western and eastern Atlantic (Cohen et al., 1990). Age classes discerned in this study also agree well with those documented by Cohen et al. (1990) for the eastern Atlantic. Age classes for the eastern Atlantic are defined as follows: 3 years at 150 mm total length (TL), 5 years at 200 mm TL, 7 years at 250 mm TL, and 9 years at 290 mm TL (Cohen et al., 1990). The maximum length of *E. cimbrius* from this study (328 mm TL) again is similar to the maximum length recorded in the western Atlantic (305 mm TL) by Cohen et al. (1990).

The Kolmogorov-Smirnoff test showed no significant difference between length-frequency distributions of observed total lengths and back-calculated lengths derived from otolith increment data. This finding further corroborates that presumed annuli in sagittal otoliths were formed at regular time intervals and can be used to assign ages to length classes.

In aging studies, it is a common technique to compare assigned ages to length-frequency modes to confirm age classes (Campana and Jones, 1992). This was not attempted because of substantial overlap in the length-frequency modes of *E. cimbrius*. Length-frequency modes with substantial overlap have proven to be unreliable as predictors of component age groups because of several factors: the number of modes may be less than the number of components, modes may be obscured or indistinct, or false modes may be generated (Beamish and McFarlane, 1987). Fourbeard rocklings spawn from May to October (Battle, 1930; Cohen et al., 1990) and overlap in the length-frequency modes is likely due to this prolonged spawning season.

After the first year, the age-length relationship of fourbeard rocklings was linear. The young grew to an average of 113 mm during the first year, and, on average, grew 24 mm per year to age 9. The relative large size and narrow size range of one-year-old fish may be attributed to the under-representation of smaller fish in the sample size. Fast early growth, like that of *E. cimbrius*, is exhibited by most gadids, and is particularly evident in red hake, *Urophycis chuss*, and white hake, *U. tenuis*. This type of growth is probably advantageous to *U. chuss* and *U. tenuis* and to other small demersal marine fishes that enter habitats dominated by larger individuals (Markle et al., 1982). Arctic cod, *Boreogadus saida*, from Labrador also exhibits growth rates similar to that of *E. cimbrius*. After reaching approximately 90 mm in their first year, *B. saida* average roughly 40 mm per year until age 5; they rarely live beyond age 6 (Lear, 1983).

Table 4

Relative importance of prey items of *E. cimbrius* according to numerical and frequency of occurrence indices. (n=36).

Prey taxon	No.	%No.	Frequency	%Frequency
Phylum Mollusca				
Class Bivalvia	183	49.1	26	72.2
Order Protobranchia	183	49.1	26	72.2
Family Nuculanidae				
Yoldia sp.	183	49.1	26	72.2
Phylum Annelida				
Class Polychaeta	6	1.6	6	16.7
Family Phyllodocidae				
Unidentified Phyllodocidae	1	0.3	1	2.8
Paranaitis sp.	2	0.5	2	5.6
Family Nereidae				
Nereis sp.	1	0.3	1	2.8
Unidentified Polychaeta	2	0.5	2	5.6
Phylum Arthropoda				
Subphylum Mandibulata				
Class Crustacea	172	46.1	36	100.0
Order Copepoda	138	36.9	8	22.2
Suborder Calanoida	138	36.9	8	22.2
Subclass Malacostraca				
Series Eumalacostraca				
Superorder Peracarida				
Order Cumacea	13	3.5	9	25.0
Eudorella truncata	1	0.3	1	2.8
Diastylis quadrispinosa	7	1.9	4	11.1
Unidentified Cumacea	5	1.3	4	11.1
Order Isopoda	2	0.5	2	5.6
Unidentified Isopoda	2	0.5	2	14.0
Order Amphipoda	5	1.6	5	13.9
Family Hyperiidea				
Unidentified Hyperiidea	3	0.8	2	5.6
Family Calliopidae				
Calliopius laeviusculus	1	0.3	1	2.8
Family Gammaridae				
Unidentified Gammaridae	2	0.5	2	5.6
Order Mysidacea	1	0.3	1	2.8
Mysidopsis bigelowi	1	0.3	1	2.8
Order Decapoda	12	3.2	11	30.6
Infraorder Caridea				
Family Crangonidae				
Crangon septemspinosa	5	1.3	4	11.1
Family Pandalidae				
Unidentified Pandalidae	1	0.3	1	2.8
Unidentified Decapoda	4	1.1	4	11.1
Infraorder Brachyura				
Unidentified Brachyura	2	0.5	2	5.6
Animal remains	11	2.9	10	27.8
Unidentified vertebrates	1	0.3	1	2.8
Number examined	36			
Number empty	3			

Total length is the most appropriate parameter to set limits around an age class for *E. cimbrius*. For example, a fish with a total length of 165 mm would be approximately 3 or 4 years old. If the weight of this same fish, approximately 15 g, was used to estimate age, the range of this estimated age would increase from 2 to 5 years. Conversely, weight appears to be a better measure of absolute growth than total

Table 5

Relative importance of prey items of 1-year-old (105–121 mm TL) (n=5) and 2–7 year old (119–271 mm TL) (n=31) *E. cimbrius* based on numerical and frequency of occurrence indices.

	105–121 mm TL				119–271 mm TL			
Prey taxon	No.	%No.	Freq.	%Freq.	No.	%No.	Freq.	%Freq.
Phylum Mollusca								
Class Bivalvia	14	19.2	4	80.0	169	56.3	22	71.0
Order Protobranchia	14	19.2	4	80.0	169	56.3	22	71.0
Family Nuculanidae								
Yoldia sp	14	19.2	4	80.0	169	56.3	22	71.0
Phylum Annelida								
Class Polychaeta	0	0.0	0	0.0	6	2.0	6	19.4
Family Phyllodocidae								
Unidentified Phyllodocidae	0		0		1	0.3	1	3.2
Paranaitis sp.	0		0		2	0.7	2	6.5
Family Nereidae								
Nereis sp.	0		0		1	0.3	1	3.2
Unidentified Polychaeta	0		0		2	0.7	2	6.5
Phylum Arthropoda								
Subphylum Mandibulata								
Class Crustacea	59	80.7	8	160.0	113	37.7	28	90.3
Order Copepoda	52	71.2	4	80.0	86	28.7	4	12.9
Suborder Calanoida	52	71.2	4	80.0	86	28.7	4	12.9
Subclass Malacostraca								
Series Eumalacostraca								
Superorder Peracarida								
Order Cumacea	4	5.4	2	40.0	9	3.0	7	22.6
Eudorella truncata	0		0		1	0.3	1	3.2
Diastylis quadrispinosa	2	2.7	1	20.0	5	1.7	3	9.7
Unidentified Cumacea	2	2.7	1	20.0	3	1.0	3	9.7
Order Isopoda	0	0.0	0	0.0	2	0.7	2	6.5
Unidentified Isopoda	0		0		2	0.7	2	6.5
Order Amphipoda	2	2.7	1	20.0	4	1.3	4	12.9
Family Hyperiidea								
Unidentified Hyperiidea	2	2.7	1	20.0	1	0.3	1	3.2
Family Calliopidae								
Calliopius laeviusculus	0		0		1	0.3	1	3.2
Family Gammaridae								
Unidentified Gammaridae	0		0		2	0.7	2	6.5
Order Mysidacea	0	0.0	0	0.0	1	0.3	1	3.2
Mysidopsis bigelowi	0		0		1	0.3	1	3.2
Order Decapoda	1	1.4	1	20.0	11	3.7	10	32.3
Infraorder Caridea								
Family Crangonidae								
Crangon septemspinosa	0		0		5	1.7	4	12.9
Family Pandalidae								
Unidentified Pandalidae	0		0		1	0.3	1	3.2
Unidentified Decapoda	1	1.4	1	20.0	3	1.0	3	9.7
Infraorder Brachyura								
Unidentified Brachyura	0		0		2	0.7	2	6.5
Animal remains	0	0.0	0	0.0	11	3.7	10	32.5
Unidentified vertebrate	0	0.0	0	0.0	1	0.3	1	3.2
Number examined	5				31			
Number empty	0				3			

length. The weight of fish between 300 mm and 325 mm TL ranged widely from 80 g to 160 g. After linear growth has slowed, fish still continue to gain weight.

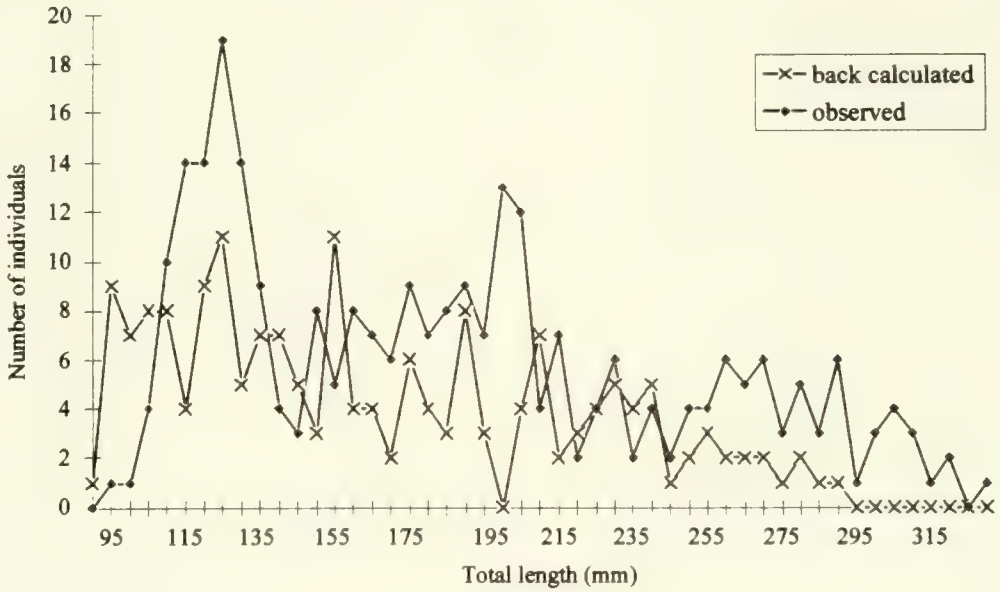


Figure 7

Length-frequency distribution of back-calculated lengths at age vs. observed lengths at age of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5.

The dietary habits of *E. cimbrius* may contribute to its constant absolute growth. Fourbeard rocklings generally forage on small animals in large numbers instead of large animals in small numbers. Fishes that swim actively and forage for small organisms (i.e. "grazers") generally have a higher unit of energy expenditure per unit of energy input than do fishes that are lie-and-wait predators on large organisms. In addition, preference for cold temperatures may explain further why *E. cimbrius* exhibits constant linear growth. I speculate that *E. cimbrius* uses its energy to forage; energy that would otherwise have contributed to absolute growth.

Table 6

Prevalence (P), abundance (A), standard error (SE), and intensity (I) of Raphidascaridinae sp., *Grillotia erinaceus*, *Genolinea laticauda*, and *Gonocerca phycidis* in *E. cimbrius* collected during the GM 93-20 and GM 94-12 surveys.

Parasite	*n*	P (%)	A ± SE	I range
Raphidascaridinae sp.	34	23.0	1.69 ± 1.24	1–32
Grillotia erinaceus	31	20.9	1.65 ± 0.25	1–8
Genolinea laticauda	7	4.7	4.33 ± 0.96	1–7
Gonocerca phycidis	1	1.4	2.00 ± 0.00	2

Dietary habits

Prey items of *E. cimbrius* surveyed in this study were predominately bivalves, particularly *Yoldia* sp., in both number and frequency. Calanoid copepods, although present in great numbers, were consumed by few individuals. The importance of copepods is replaced by bivalves, *Yoldia* sp., and polychaetes in the diet of larger fish (>119 mm TL). After their first year, fish shift from a diet dominated by planktonic copepods to a diet comprising infauna (bivalves and polychaetes).

Calanoid copepods composed the majority (71.2%) of the prey taken, with bivalves (although consumed in relatively high frequency (80.0%)) second in importance by number (19.2%) in 1-year-old fish. Juveniles in the present study exhibited feeding preferences for various calanoid copepods similar to those of pelagic larval gadids off the Isle of Man (Nagabhushanam, 1965.) This preference for planktonic organisms suggests that juveniles lead a less sedentary existence and feed more frequently in the water column than do adults. In addition, the selection for smaller prey is directly related to mouth size (Moyle and Cech, 1988).

On Georges Bank, fourbeard rocklings >100 mm TL consumed motile epifauna, particularly *Crangon septemspinosa* (46.3%), in the highest percentage by

Table 7

Prevalence of infection (P%) and abundance (A) of four species of helminths in age-class ranges from *E. cimbrius* collected during the GM 93-20 and GM 94-12 surveys. (n=148).

		Raphidascaridinae sp.		*G. erinaceus*		*G. laticauda*		*G. phycidis*	
Age class	n	P(%)	A	P(%)	A	P(%)	A	P(%)	A
1	12	8.3	0.1	16.7	0.2	0.0	0.0	0.0	0.0
2	11	9.1	0.5	9.1	0.2	9.1	0.2	9.1	0.2
3	20	20.0	0.3	25.0	0.3	0.0	0.0	0.0	0.0
4	51	21.6	1.3	17.6	0.2	5.9	0.2	0.0	0.0
5	27	26.0	2.3	14.8	0.4	3.7	0.2	0.0	0.0
6	15	26.7	1.9	20.0	0.4	6.7	0.5	0.0	0.0
7	8	37.5	1.5	37.5	0.4	0.0	0.0	0.0	0.0
8	2	50.0	1.0	100.0	1.5	0.0	0.0	0.0	0.0
9	2	100.0	2.5	100.0	2.5	0.0	0.0	0.0	0.0

weight followed by animal remains (30.1%) and infauna, primarily polychaetes (13.6%) (Langton and Bowman, 1980). Decapod crustaceans were not as important as these other groups to juvenile fish in the present study. Decapods appeared in number for the first time in 2- to 7-year-old fish. This can be explained by the preference for larger prey by older, larger fish.

In a Norwegian fjord, *E. cimbrius* between 70 and 300 mm TL preyed primarily on crustaceans, polychaetes, fish, bivalves and rarely on copepods (Mattson, 1981). In adult rocklings, high percentages of infauna, particularly polychaetes, have been reported from the North Sea (Moller-Buchner et al., 1984) and Passamaquoddy Bay, where the frequency was found to be correlated with an increase in fish size (Keats and Steel, 1990). The high frequency of infaunal organisms, predominantly bivalves, in the diet of 2- to 7-year-old fish in the present study exhibits a similar trend. This finding may be correlated with adults having a sedentary existence and remaining in close contact with the substrate (Bigelow and Schroeder, 1953; Cohen et al., 1990). This lifestyle, compounded with the fact that this species has well-developed stout barbels equipped with taste buds (Nagabhushanam, 1965), would enable larger fish to feed more effectively on epifauna and infauna.

E. cimbrius is best characterized as a euryphagous bottom-rover or "grazer." (Moyle and Cech, 1988). The size of the prey appears to be directly correlated with the size of the predator as seen in the change in diet from 1-year-old fish to those 2 to 7 years of age.

Parasitism

The parasite fauna of *E. cimbrius* consisted of three taxa and four species: Nematoda (1), Cestoda (1), and Trematoda (2). The prevalence (P%) and abundance (A) of a nematode from the subfamily Raphidascaridinae (probably *Hysterothylacium*) and a trypanorhynch cestode, *G. erinaceus*, appear to increase with fish age. The P% and A of both digenetic trematodes were low in all age classes.

The few helminths found were in low abundance. This is uncommon because other gadids are known to have abundant and diverse parasite faunas (Margolis and Arthur, 1979). The very low parasite diversity of *E. cimbrius* supports evidence of limited movements and benthic feeding preferences in its habitat.

All nematode specimens of the subfamily Raphidascaridinae were second- or third-stage and third- or fourth-stage larvae (Measures[1]). The presence of parasites in the same stage of development are indicative of a "grazer" (Dogiel, 1966) and provides additional support to characterize *E. cimbrius* as such. A similar trend is seen in *G. morhua*, where its mode of life, generalist feeding habits, and association with the bottom facilitate the infestation by *Raphidascaridinae* spp. (Dogiel et al., 1970).

The increase in prevalence of *Grillotia erinaceus* from 9.1% at 2 years to 25.0% at 3 years appears to be correlated with the an increase of arthropods in the diet. In the life cycle of *G. erinaceus*, the plerocercus larvae can be acquired by an intermediate teleost host through consumption of arthropods, mainly copepods, which have previously ingested the tapeworm eggs (Sakanari and Moser, 1985). It is not possible to draw any firm conclusions on this relationship because food habit data in this study did

[1] Measures, L. 1995. Maurice Lamontagne Institute, Fisheries and Oceans, Mont-Joli (Quebec), Canada G5H 3Z4. Personal commun.

not account for seasonal variation and because the sample size of 8- and 9-year-old fish was low.

The definitive hosts of adult trypanorhynchs are elasmobranchs, suggesting that fourbeard rocklings are consumed by elasmobranchs or act as paratenic hosts. It is likely that barndoor skate, *Raja laevis*, and thorny skate, *Raja radiata*, prey upon *E. cimbrius*. *Raja laevis* and *R. radiata* >700 mm TL forage primarily on fish that include hake, *Urophycis* spp., and whiting, *Merluccius* spp., and may also feed on cod and haddock (Bigelow and Schroeder, 1953; McEachran et al., 1976). Because both *Raja* spp. consume fishes with similar habits and are definitive hosts for *G. erinaceus* (Margolis and Arthur, 1979), it is probable that *R. laevis* and *R. radiata* prey upon *E. cimbrius*.

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Genetic identification of sharks in the U.S. Atlantic large coastal shark fishery*

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Abstract.—Nucleotide sequences of a 394–396 base pair fragment of mitochondrial (mt) DNA, including parts of the cytochrome *b* and threonine tRNA genes, were obtained for eleven species of carcharhiniform sharks important to the U.S. Atlantic large coastal shark fishery. Sequences were used to predict sizes of restriction fragments produced by 118 restriction enzymes with unique recognition sequences. Seven restriction enzymes were chosen that produce an array of species-specific fragments for the eleven species. Geographic variation was examined in several species by surveying specimens from geographically distant regions. Only one of the species, the spinner shark *(Carcharhinus brevipinna),* exhibited geographic variation in mtDNA restriction fragments. The sandbar shark (*C. plumbeus*) exhibited sequence polymorphism that did not produce differences in restriction patterns of any of the seven enzymes. We detected numerous differences between observed restriction patterns in ten tiger sharks (*Galeocerdo cuvier*) and patterns predicted from a published sequence. We concluded that the published sequence is incorrect. Amplification of a single PCR product from a sample of meat, digestion of aliquots of the product with restriction enzymes, and sizing of fragments on agarose gels is an efficient method for distinguishing among these eleven carcharhiniform sharks. The method can be applied when only a small amount of tissue is available.

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The U.S. Atlantic large coastal shark fishery grew rapidly during the 1980s when commercial landings increased from 135 metric tons (t) in 1979 to a high of 7122 t in 1989 (NMFS, 1993). In 1993, a quota of 2750 t was established; in 1997 this quota was halved to 1375 t in order to rebuild depleted shark stocks. This fishery targets several species of sharks that are valued for fins (exported to Asia) and meat (sold domestically). Because of the slow growth rate, high age at maturity, and low fecundity of most shark species (Pratt and Casey, 1990), commercial shark fisheries typically collapse after a brief period unless strict conservation measures are implemented (Holden, 1974, 1977; Hoenig and Gruber, 1990). The 1993 shark fishery management plan divided exploited species into three categories: large coastal sharks, small coastal sharks, and pelagic sharks (NMFS, 1993). The category that grew most rapidly was the large coastal shark fishery, which is dominated by several species of requiem sharks and two species of hammerhead sharks.

Sound management of a multispecies fishery requires information on the vulnerability of each component of the fishery. Differences in life history characters, e.g. intrinsic growth rates, locations of nursery areas, or migration within or outside of the fished area, can result in different vulnerabilities to overfishing of exploited species. For example, Musick et al. (1993) reported a relative decline in the dusky shark (*Carcharhinus obscurus*) off Virginia during expansion of the large coastal shark fishery. Thus, it is important to estimate catches on a species-by-species basis and to implement species-specific management. In the event that regulations (e.g. moratoria or minimum size limits) are applied to individual species, enforcement will rely on identification of protected species within the catch. The manner in which sharks are processed at sea, however, makes it difficult to accurately identify species at landing. Sharks typically are headed, gutted, and finned (i.e. fins are removed), thus destroying morphological characters necessary for species identification. Although Castro (1993) recommended a suite of characters for identification of shark carcasses, the limited number of available morphological characters makes it difficult to distinguish among several species. Martin (1993) suggested that use of restriction-frag-

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ment differences in polymerase chain reaction (PCR) amplified DNA might provide a rapid and inexpensive means of identifying carcasses and fins. We develop this technique as a means of identifying the eleven most frequently landed carcharhiniform sharks in the U.S. east coast longline fishery.

Materials and methods

Tissues (heart, white muscle, or fin) from nine species of carcharhinid sharks and two species of sphyrnid sharks were obtained from commercial fishermen, sport tournaments, and research longlining cruises (Table 1). Tissues were either frozen in the field and stored at –80°C or preserved immediately in 10× Longmire's lysis buffer (0.1 M tris, 0.1 M Na_2EDTA, 0.01 M NaCl, 0.5% SDS, pH 8.0) at room temperature. Genomic DNA was isolated by first powdering tissue under liquid nitrogen with a prechilled mortar and pestle. Approximately 100 mg of powdered tissue were suspended in 500 µL STE buffer (0.1 M NaCl, 50 mM tris, 1 mM EDTA; pH 7.5) and lysed with 25 µL 20% SDS. Genomic DNA was extracted twice with phenol:chloroform:isoamyl alcohol (25:24:1) and twice with chloroform:isoamyl alcohol (24:1). DNA in aqueous phase was precipitated by adding 2.5 volumes of ice-cold absolute ethanol and 0.1 volumes of 3M NaOAC, stored at –20°C for at least two hours, centrifuged for 15 min at 4°C at maximum speed in a microcentrifuge, and rinsed with 70% ethanol.

PCR amplification for cycle sequencing or restriction-enzyme digestion was accomplished by using a suite of PCR primers. The "diagnostic" fragment used in digestions consisted of a single segment, 394–396 bp in length, that was amplified by using light-strand primer Cb3RL (CATATTAAACCCGAATGATAYTT) located within the 3' domain of the mitochondrially encoded cytochrome *b* (cyt *b*) gene and heavy-strand primer Cb6H (CTCCAGTCTTCGRCTTACAAG) located within the mitochondrially encoded threonine tRNA ($tRNA^{THR}$) gene (Martin and Palumbi, 1993). This fragment was sequenced through the primer sites by using additional primer sets within and outside the diagnostic fragment. PCR fragments were prepared for sequencing by using the Bio-Rad Prep-a-Gene DNA purification system that removes extraneous salts, primers, and small fragments of DNA prior to cycle sequencing. Dideoxy DNA sequencing was performed with the Promega *fmol* DNA sequencing system by using ^{32}P end-labeled primers. Cycle sequencing reactions consisted of a single two-minute denaturing process at 95°C, followed by thirty cycles of 1 min at 95°C, 30 sec at 64°C, and 30 sec at 72°C. Sequencing reactions were scored on 6% denaturing

Table 1

Sources of tissues or DNA sequences. EMBL/Genbank accession numbers identify sequences from Martin and Palumbi (1993).

Species	Acronym	Source of sequence	Source of specimen
Bignose shark (*Carcharhinus altimus*)	Cal-A	This study	Virginia, Atlantic Ocean
Blacktip shark (*C. limbatus*)	Cli-A	"	Virginia, Atlantic Ocean
Bull shark (*C. leucas*)	Cle-A	"	Florida, Gulf of Mexico
Dusky shark (*C. obscurus*)	Cob-A	"	Virginia, Atlantic Ocean
Sandbar shark (A) (*C. plumbeus*)	Cpl-A	GenBank L08032	Hawaii, Pacific Ocean
Sandbar shark (B)	Cpl-B	This study	Florida, Gulf of Mexico
Sandbar shark (C)	Cpl-C	"	Hawaii, Pacific Ocean
Silky shark (*C. falciformis*)	Cfa-A	"	Hawaii, Pacific Ocean
Spinner shark (A) (*C. brevipinna*)	Cbr-A	"	Pacific Ocean, Australia
Spinner shark (B)	Cbr-B	"	Virginia, Atlantic Ocean
Lemon shark (*Negaprion brevirostris*)	Nbr-B	GenBank L08039	Florida, Atlantic Ocean
"Tiger shark" (A)[1] (*Galeocerdo cuvier*)	Gcu-A	GenBank L08034	Hawaii, Pacific Ocean
Tiger shark (B)	Gcu-A	This study GenBank AF004288	Florida, Gulf of Mexico
Great hammerhead (*Sphyrna mokarran*)	Smo-A	"	Florida, Gulf of Mexico
Scalloped hammerhead (*S. lewini*)	Sle-A	GenBank L08041	Hawaii, Pacific Ocean

[1] It was determined that this sequence was not tiger shark (see text)

polyacrylamide gels and examined by autoradiography. DNA sequences were read on an IBI gel reader and entered directly into computer text files. Sequences were confirmed by recording a minimum of two separate sequencing runs through each base. Sequences were aligned by using the ESEE software package (Cabot and Beckenback, 1989). Four cyt *b* sequences—those of sandbar (*C. plumbeus*), lemon (*Negaprion brevirostris*), tiger (*Galeocerdo cuvier*), and great hammerhead sharks (*Sphyrna mokarran*)—were downloaded from the EMBL/NCBI Genbank database (Martin and Palumbi, 1993). All other cyt *b* sequences and all $tRNA^{THR}$ sequences were acquired from our laboratory.

Sequences from each species between primers Cb3RL and Cb6H were concatenated with sequences of the primers to produce a single sequence for each of the eleven species (Table 2). Sequences were examined for predicted restriction sites with IBI MacVector software (IBI Mac Vector, 1991). One hundred eighteen restriction enzymes with unique recognition sequences were used in the search for restriction sites.

Amplified "diagnostic" fragments were prepared by amplifying genomic DNA at thirty cycles of 95°C for 1 min, 48 to 52°C for 30 sec, and 72°C for 30 sec. Amplified fragments were ethanol precipitated as above and reconstituted in water. Generally, one 100 µL PCR reaction produced enough diagnostic fragment for all seven restriction digestions. Fragments were digested by using manufacturer's buffers and specifications. Most restriction patterns were scored on 2% agarose gels run on 1X TAE. Fragments between 40 and 100 bp were scored on either vertical nondenaturing polyacrylamide gels or 2% nusieve 3:1 agarose gels. Fragments less that 40 bp were not scored, although loss of fragments as small as 24 bp could be inferred from mobility shifts in larger fragments. All gels were stained with ethidium bromide and examined under UV light (Sambrook et al., 1989).

Results

A single mtDNA fragment of 394–396 bp that contained the 3' end of cyt *b* and part of the $tRNA^{THR}$ gene was amplified in all species. Except for two hammerhead sharks, the fragment was 395 bp in length (Table 2). Cyt *b* sequences from all eleven species were identical in length and unambiguously aligned. In comparison with the other nine species, the scalloped hammerhead (*S. lewini*) possessed a single-base deletion in the $tRNA^{THR}$ sequence, and the great hammerhead possessed a single-base insertion in the $tRNA^{THR}$ sequence.

In bignose shark (*C. altimus*), three fragments of sizes 395 bp, 720 bp, and 1040 bp were produced repeatedly. The additional bands were more pronounced at lower (48°C) than higher (52°C) annealing temperatures. Further investigation with additional primers revealed that bignose shark possessed a much larger mitochondrial D-loop region than any other shark in the study. Amplification with a light-strand primer located within cyt *b* and a heavy-strand primer located within the 12S ribosomal RNA gene produced an approximately 1400-bp fragment in all species except bignose shark, where a single fragment of approximately 2000 bp was produced. We hypothesize that the Cb6H recognition site within the $tRNA^{THR}$ gene is duplicated twice within the D-loop of the bignose shark, resulting in a three-banded amplification product. Duplication of segments of flanking regions within the mitochondrial D-loop have been reported in other vertebrates (Broughton and Dowling, 1994, and citations within). To our knowledge, this is the first evidence of this phenomenon in elasmobranchs. To obtain the single product for sequencing and restricting, the 395-bp fragment was excised from an agarose gel and reamplified to produce sufficient amounts of the diagnostic fragment.

Of 118 restriction enzymes surveyed by MacVector software, 34 were predicted to have restriction sites within one or more of the eleven species. Seven restriction enzymes (*Alu*I, *Dde*I, *Fok*I, *Hae*III, *Hinc*II, *Hinf*I, and *Rsa*I) were chosen for screening because use of these seven enzymes allowed all eleven species to be distinguished (Table 3). The number of sharks whose mtDNA was subjected to restriction-enzyme digestion is given in Table 4. The initial screen of restriction sites was undertaken with only a single sequence from each species. Differences in predicted and observed restriction patterns in three species (sandbar, spinner, and tiger sharks) made it necessary to sequence additional animals in order to investigate whether differences were due to sequencing errors or intraspecific variation.

Observed restriction patterns in sandbar sharks from the Gulf of Mexico differed by restriction site from the pattern predicted from the published sequence of Martin and Palumbi (1993) for a sandbar shark (Cpl-A) from Hawaii (Martin[1]). Although we predicted that *Fok*I would not cut the sandbar shark fragment, *Fok*I digestion produced two fragments of 310 and 85 bp. We sequenced additional sandbar sharks from the Gulf of Mexico (Cpl-B) and from Hawaii (Cpl-C) and found that both sequences possessed the *Fok*I restriction site. Sequence of the speci-

[1] Martin, A. P. 1997. University of Nevada-Las Vegas, Las Vegas, NV 89154-4004. Personal commun.

Table 2

DNA Sequences used to predict restriction digests. Boxes surround primer sequences used in PCR amplification (A=adenine, C=cytosine, G=guanine, T=thymidine, Y=C or T). A vertical line is drawn between the end of the cytochrome *b* sequence and the beginning of the threonine tRNA sequence. See Table 1 for description of samples.

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          5'  Cb3RL  ->

Cal-A     CATATTAAACCCGAATGATAYTT CTTATTTGCTTATGCAATCCTGCGCTCAATCCCTAATAAACTAGGAGGAGTCCTAGC
Cbr-A     ....................... ...........C......T.A.............C.....................
Cbr-B     ....................... ...........C......T.A.............C.....................
Cfa-A     ....................... ......C.....C......T.A........T.......................
Cle-A     ....................... ....................A...........C.......................
Cli-A     ....................... ......C..C...........A........T.......................
Cob-A     ....................... ..................TT.A...........C.....................
Cpl-A     ....................... ...........................................................
Cpl-B     ....................... ...........................................................
Cpl-C     ....................... ...........................................................
Gcu-A     ....................... .C.......C.........T.C..G...........C.....................
Gcu-B     ....................... ..................T.A..T..T.....C..................T.....
Nbr-A     ....................... .........C...........A.....T..T.....C.....................
Sle-A     ....................... .C....C..C.........T.A.....T..T.....C................T....
Smo-A     ....................... ......C..C.........T.A.....C..T.....C.....................

Cal-A     TCTCCTATTCTCTATCTTCATCCTTATATTGGTGCCCCTCCTCCACACCTCCAAACAACGAAGTACCATCTTCCGACCCA
Cbr-A     C..............T..T.....C.....A..C..T.........T.....................T.............
Cbr-B     C..............T..T.....C.....A..C..T.........T.....................T.............
Cfa-A     ........................C.........T..T.............................C.........T.......
Cle-A     C.........T..C..T..T...........A..T..T.....................................T.
Cli-A     ............C.....T...........AA.T..T..............T.............................T
Cob-A     C............G.....T.....C.....A..T..T.............................C...G.............
Cpl-A     ....................T.....................................................
Cpl-B     ...........................................................................
Cpl-C     ...........................................................................
Gcu-A     C.........T.....TC.T...........A..T..T.....T..A.....T.........................A.
Gcu-B     C..AG..........T.........C...C.AA.T..T..T...........T...........C.G..C.........AAC
Nbr-A     C............C..T.........C...C.A..C.....T...........A.............T...........TC
Sle-A     C..TT.......A.....T.....C...C.A..T..A..A..T.......................A............AC
Smo-A     ............C.....T.....C...C.A..C.TTTA...T.........T.............A............AC
```

continued

men from the Gulf of Mexico (Cpl-B) differed from that of the specimen from Hawaii (Cpl-C) by three base-pair substitutions. The sequence from the specimen from Hawaii (Cpl-C) differed from that of Martin and Palumbi (1993) by one base-pair (and which affected the *Fok*I restriction site). Whether the single base pair difference between our specimen from Hawaii and the one reported in Martin and Palumbi (1993) represents an uncommon polymorphism in sandbar sharks from the Pacific or an error in reading the original sequence cannot be determined. We examined restriction digestions from three sandbar sharks collected near Hawaii and all possessed the *Fok*I restriction site.

We also found a populational difference between spinner sharks (*C. brevipinna*) collected from the North Atlantic (including the Gulf of Mexico) and from the Pacific coast of Australia. Initially, we sequenced a spinner shark from Australia and predicted that *Rsa*I would not cut the diagnostic fragment. We restricted fragments from seven spinner sharks, two from Australia, and five from the U.S. Atlantic and Gulf of Mexico coasts. Although fragments from the two spinner sharks from Australia were not cut with *Rsa* I, each of the five specimens from the Atlantic produced fragments of 251 and 144 bp. We sequenced one specimen from the Atlantic (spinner B) and found two nucleotide substitutions, including one that resulted in the restriction site difference between spinner sharks from the Atlantic and Pacific.

We detected numerous differences between restriction patterns predicted from the sequence of Martin and Palumbi (1993) for tiger shark collected near Hawaii and our tiger sharks collected from the Gulf of Mexico (Atlantic) and Hawaii and Australia (Pacific).

Table 2 (continued)

```
Cal-A   TAACACAAATCTTCTTCTGACTTCTTGTGGCCAACTCAATTATTTTAACTTGAATTGGAGGTCAACCAGTAGAACAACCA
Cbr-A   ..........T.................A..T..T.............................C..................
Cbr-B   ..........T.................A..T..T.............................C..................
Cfa-A   ........................C..A................C.................C..................
Cle-A   ..........TC............C..A..T..T.........................T.....................
Cli-A   ............................A..T..T.....C.............................C............
Cob-A   ...G........................A.....T.............................C..................
Cpl-A   ...........................................................................................
Cpl-B   ...........................................................................................
Cpl-C   ...........................................................................................
Gcu-A   ....C......C........T.C.....A..T........C..CC................C..................
Gcu-B   .T........................C..A..T..................C...........A..................
Nbr-A   .C..................T.......A..T.............................C..................
Sle-A   ........................C..A..............CC................C..................
Smo-A   ....................T.....C.A..T...........C.....C.............................

Cal-A   TTCATTATAGTAGGACAAATCGCCTCAATCTCCTACTTTTCCTTATTCCTTATTATTATACCATTCACTAGCTGATGAGA
Cbr-A   ....................T..T.................................C..C.....T..T..C............
Cbr-B   ....................T..T.................................C..C.........T..C............
Cfa-A   ..T.....................................G.................................C.........C..
Cle-A   .......C............T.....................................C.........T...............
Cli-A   ...................................................T......G.C.........................
Cob-A   ..............T.....................................C..C......C.T...............
Cpl-A   ....................T.....................................C...............
Cpl-B   ...........................................................................................
Cpl-C   ....................T.....................................C...............
Gcu-A   ....................T.....................A....T...........T......G.C.........C..
Gcu-B   ..T....C............T..T.....................T.....C..C.........T.TC.........C..
Nbr-A   ..T.....................T.....................................T...........T..
Sle-A   ..T....C.................................C..TC....T.....C.............G.C.........C..
Smo-A   ..T.....................................A..........C.............G..........C..

Cal-A   AAACAAAATCCTCAGCCTAAATTAG TTTTGGTAACTTAACT-AAAAAGCGTCGAC CTTGTAAGYCGAAGACTGGAG
Cbr-A   ......................... .........G..................... ....................
Cbr-B   ......................... .........G..................... ....................
Cfa-A   ...T..................... .........G..................... ....................
Cle-A   ......................... .........G..................... ....................
Cli-A   ......................... .........G..................... ....................
Cob-A   ......................... .........G..................... ....................
Cpl-A   ......................... .........G..................... ....................
Cpl-B   ......................... .........G..................... ....................
Cpl-C   ......................... .........G..................... ....................
Gcu-A   .........T...........C... .........G..................... ....................
Gcu-B   ....................C... .........G..................... ....................
Nbr-A   ...T..................... .........G..................... ....................
Sle-A   .........T...........C... ........GG........-............ ....................
Smo-A   .........T...........C... ........GG.....T.CGT........... ....................

                                                                  <-  Cb6H  3'
```

We sequenced a tiger shark from the Gulf of Mexico and found 46 nucleotide differences between our sequence and that of Martin and Palumbi (1993). This difference is greater than that seen between all pairs of species in this study and is clearly too large of a difference to be explained by intraspecific polymorphism. Because our observed restriction patterns for tiger sharks from the Atlantic and Pacific match predictions made from our tiger shark sequence, our sequence for the tiger shark is likely correct, and part of the sequence listed in Martin and Palumbi (1993) is not that of tiger shark.

The remaining eight species—bignose, blacktip (*C. limbatus*), bull (*C. leucas*), dusky, silky (*C. falciformis*), scalloped hammerhead, great hammerhead, and lemon sharks—exhibited restriction patterns

identical to those predicted based on sequence data (Table 4). The list of species that showed no variation in restriction pattern included silky and dusky sharks from widely disparate geographic locales.

Discussion

Restriction digests of the diagnostic 394–396 bp fragment proved a reliable way to distinguish among the

Table 3

Predicted restriction fragments for seven enzymes based on nucleotide sequences.

Species	*Alu*I	*Dde*I	*Fok*I	*Hae*III	*Hin*cII	*Hin*fI	*Rsa*I
Bignose	232, 84, 79	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Blacktip	121, 111, 79, 43, 41	333, 64	395	395	223, 148, 24	324, 71	251, 144
Bull	190, 121, 43, 41	331, 64	395	395	223, 148, 24	324, 71	251, 144
Dusky	311, 43, 42	331, 64	395	221, 174	371, 24	324, 71	395
Sandbar A	223, 79, 43, 41	331, 64	395	205, 190	223, 148, 24	324, 71	251, 144
Sandbar B	223, 79, 43, 41	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Sandbar C	223, 79, 43, 41	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Silky	232, 79, 43, 41	331, 64	310, 85	221, 174	371, 24	324, 71	395
Spinner A	190, 121, 43, 41	331, 64	395	221, 174	371, 24	324, 71	395
Spinner B	190, 121, 43, 41	331, 64	395	221, 174	371, 24	324, 71	251, 144
Lemon	190, 121, 43, 41	331, 64	310, 85	221, 174	371, 24	324, 71	395
"Tiger" A[1]	190, 121, 43, 41	331, 64	208, 187	221, 174	371, 24	216, 108, 71	251, 144
Tiger B	190, 121, 43, 28, 13	331, 64	310, 85	395	371, 24	395	395
Great Hammerhead	121, 111, 85, 89	331, 65	396	396	223, 149, 24	325, 71	396
Scalloped Hammerhead	311, 83	256, 75, 63	394	221, 173	370, 24	323, 71	395

[1] It was determined that this sequence was not that of a tiger shark. See text

Table 4

Number and location of sharks whose mtDNA was subjected to restriction enzyme digestion. Numbers in parentheses represent number of sharks from each source location in the sample.

Species	*n*	Source of specimen
Bignose shark	4	Virginia, Atlantic Ocean (4)
Blacktip shark	7	Virginia, Atlantic Ocean (1); Florida, Gulf of Mexico (6)
Bull shark	7	Florida, Gulf of Mexico (7)
Dusky shark	7	Virginia, Atlantic Ocean (2); Florida, Atlantic Ocean (1); Australia, Pacific Ocean (3); Australia, Indian Ocean (1)
Lemon shark	7	Florida, Gulf of Mexico (6); Mexico, Gulf of Mexico (1)
Sandbar shark	10	Florida, Gulf of Mexico (7); Hawaii, Pacific Ocean (3)
Silky shark	7	Texas, Gulf of Mexico (3); Hawaii, Pacific Ocean (4)
Spinner shark	7	Virginia, Atlantic Ocean (1); Florida, Atlantic Ocean (3); Florida, Gulf of Mexico (1); Australia, Pacific Ocean (2)
Tiger shark	10	Florida, Gulf of Mexico (5); Australia, Pacific Ocean (2) Hawaii, Pacific Ocean (3)
Great hammerhead	7	Florida, Gulf of Mexico, Florida (6); Florida, Atlantic Ocean (1)
Scalloped hammerhead	7	Virginia, Atlantic Ocean (1); Florida, Gulf of Mexico (2); Alabama, Gulf of Mexico (1); Texas, Gulf of Mexico (1); Campeche, Gulf of Mexico (2)

eleven species of carcharhiniform sharks. Each species possessed a unique set of restriction fragments, and even in the species where polymorphism was detected, misidentification was not a problem. This technique can be performed on small pieces of tissue collected at dockside and stored indefinitely at room temperature and moreover can distinguish between species whose carcasses may be difficult to discriminate (Fig. 1). Similar DNA technology has been used for identifying carcasses in teleosts (Chow et al., 1993; Bartlett and Davidson, 1991), and for identifying planktonic fish eggs (Daniel and Graves, 1993)—cases where morphological characters proved insufficient for species level identification .

Use of genetic characters to identify species can be complicated by population structure. Although most marine fishes that are distributed across vast geographic stretches are open-ocean pelagics (Briggs, 1960), with presumed minor genetic differences across the range of a species (but see Crosetti et al., 1994; Graves et al., 1992), many large coastal sharks are distributed as multiple discrete populations (Compagno, 1984). It is thus important to know whether genetic differences among individuals are diagnostic of species or populations. Some questions, among others, are the following: to what degree are published genetic data useful in regions other than those from which the original specimens were collected, and can this method be used to identify populations as well as species? Baker et al. (1996), for example, were able to determine geographic origin of marine mammals they identified from flesh samples on the basis of genetic data. In our study, regional differences in restriction patterns were observed in only one species, spinner shark, whereas sequence differences that did not affect restriction patterns were observed in sandbar shark. In four species (dusky, silky, scalloped hammerhead, and tiger), sequences from one individual accurately predicted restriction sites in specimens collected thousands of kilometers from where the original specimen was collected.

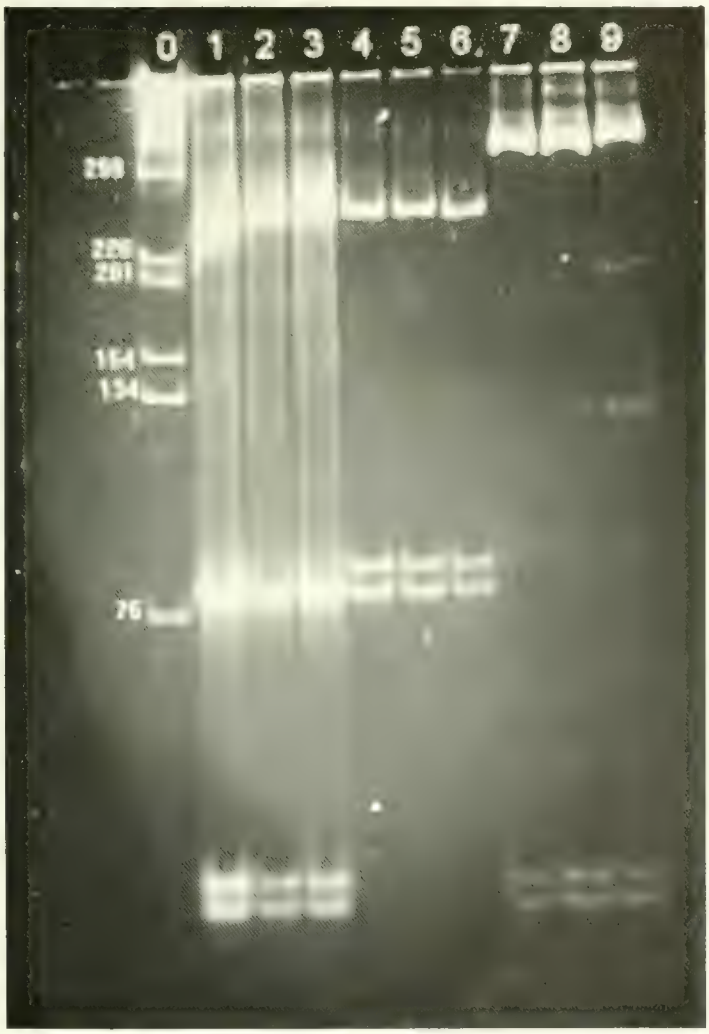

Figure 1

Ten-percent polyacrylamide gel of *Alu*I digests in three species that produce very similar carcasses. Lane zero is a size standard, lanes one to three are sandbar sharks, lanes four to six are bignose sharks, and lanes seven to nine are dusky sharks. Numbers at left refer to sizes (base pairs) of size standards. Predicted sizes of fragments in each species are given in Table 3.

The low level of intra- and interregional polymorphism within species is not surprising given the low genetic diversity typically reported for sharks (Smith, 1986). In restriction fragment length polymorphism (RFLP) studies of whole mtDNA molecules, Heist et al. (1995, 1996) found a very low nucleotide sequence diversity of 0.036% in sandbar shark and 0.13% in Atlantic sharpnose shark (*Rhizoprionodon terraenovae*). The small numbers of substitutions between geographically distant populations of sandbar and spinner shark observed in this study indicate that intraspecific diversity should not hinder species identification of these eleven species.

The erroneous tiger shark sequence in the study of Martin and Palumbi (1993) indicates a further strength of the PCR-RFLP technique beyond use for forensic identification; it can be used to evaluate

validity of sequence data. Many molecular genetic or phylogenetic studies (or both) are based on sequences sampled from only one individual of a species. Discovery of erroneous sequence data in such studies is becoming increasingly common (Derr et al., 1992; Helbig and Seibold 1996; Ledje and Arnason, 1996). PCR reactions are easily contaminated by carryover DNA from other organisms or by other DNAs in the laboratory (Thomas, 1994). Mislabeling of tubes also can lead to incorrect assignment of sequence data to species. We sequenced the entire cyt *b* gene in tiger shark from Florida and, in comparison with the "tiger shark" sequence reported by Martin and Palumbi (1993), found one nucleotide difference in the first (5'-most) 540 bp of the gene and 64 nucleotide differences in the remaining 606 bp of the gene. We hypothesize that the "tiger shark" sequence of Martin and Palumbi (1993) is a mixture that includes sequence data from another species. The discrepancy between published and newly determined sequences is similar to observations on published bird sequence by Helbig and Seibold (1996) and on mammalian sequences reported by Ledje and Arnason (1996). In each case, the published sequences differed so greatly from newly obtained sequences that conclusions of the prior works were called into question. The free exchange of sequence data through Genbank also facilitates replication of errors. Validity of sequence data can, and perhaps should, be tested by amplifying DNA from several individuals of the same species, and then by determining whether predicted restriction sites are present in all amplifications.

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Influence of temperature and effort on lobster catches at different temporal and spatial scales and the implications for stock assessments

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Abstract.—Correlation analysis was used to investigate how effort and temperature changes influence lobster catches at different spatial and temporal scales and how they may affect the use of catch statistics in stock assessments. At the largest scales examined (Atlantic coast of Nova Scotia, 50 yr), a significant correlation between catches and temperatures at short lags (0–3 yr) prior to 1974 suggests that catches were driven by temperature-induced changes in growth or lobster activity. However, changes in effort could not be ruled out as a cause of the observed cycles because sea surface temperatures may reflect weather conditions and the "fishability" of the grounds. Longer lags (6–8 yr) after 1974 are consistent with increased larval survival due to sharply rising temperatures and the "recruitment pulse" of the late 1980s. There was no clear relation between temperature and catches at intermediate scales (statistical districts, 10 yr), but effort changes indicate that catches alone do not accurately reflect changes in lobster abundance. At the smallest scale examined (distances between ports, days) correlations of both temperature and effort with catch in areas with similar coastal topographies indicated that the correlation between temperature and catch was not causative, i.e. changes in effort, were driven by wind events that were also influencing water temperatures. The results indicate that effort changes must be considered at all scales in stock assessments, but they become increasingly important at the smallest (i.e. <100 km, within years) scales. They also indicate that significant correlations between lobster catches and environmental parameters must be interpreted cautiously.

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In the absence of suitable effort data, long-term, large-scale changes in American lobster (*Homarus americanus*) populations are generally assessed by using summarized catch statistics (e.g. Harding et al, 1983; Pezzack, 1992; Drinkwater et al, 1991, 1996), under the assumption that catch trends reflect abundance changes. Two observations support this assumption. First, high exploitation rates in most areas probably remove the majority of animals recruiting to the fishery in any year (Miller et al, 1985). Second, similar catch trends over large areas of the Northwest Atlantic suggest a similar population response to a common environmental influence (Pezzack, 1992). Given that this assumption is correct at these large scales, it is of fundamental interest in survey design and data aggregation decisions to determine the spatial and temporal scales at which this assumption holds. For example, can the catch statistic alone be used to assess changes in lobster populations between, say, adjacent ports within seasons?

To understand the spatial and temporal variability of lobster catches on the Atlantic coast of Nova Scotia, Canada, and the underlying causes of this variability, I examined the influence of effort and an important environmental factor (temperature) on commercial lobster catches at different spatial and temporal scales. Temperature can affect lobster catches in the short term by altering the availability of lobsters to traps, i.e. by changing lobster behavior on the grounds (McCleese and Wilder, 1958) or by increasing growth of prerecruits to commercial sizes. In the long term it could also affect population growth by influencing survival of larvae or juvenile stages (Aiken and Waddy, 1986). Changes in effort affect lobster catches directly but how these changes occur is complex. In a lucrative fishery with a relatively short (approx. 60 d) open season and restrictions on the number of traps, fishermen tend to take the maximum number of lobsters possible with their gear. Consequently, changes in effort are more likely to be due to factors that decrease effort. For example, fishermen could decrease the number of traps fished and frequency of hauls when catches are too low to make fishing worthwhile. Because the fishery is conducted from small boats, adverse weather conditions will also decrease effort. Conversely, fishermen may respond to increasing catch rates or good weather by fishing harder. Because catches alone are often used as an indication of stock status, it is important to understand how changes in effort may be influencing catches at the different spatial and temporal scales at which assessments are conducted.

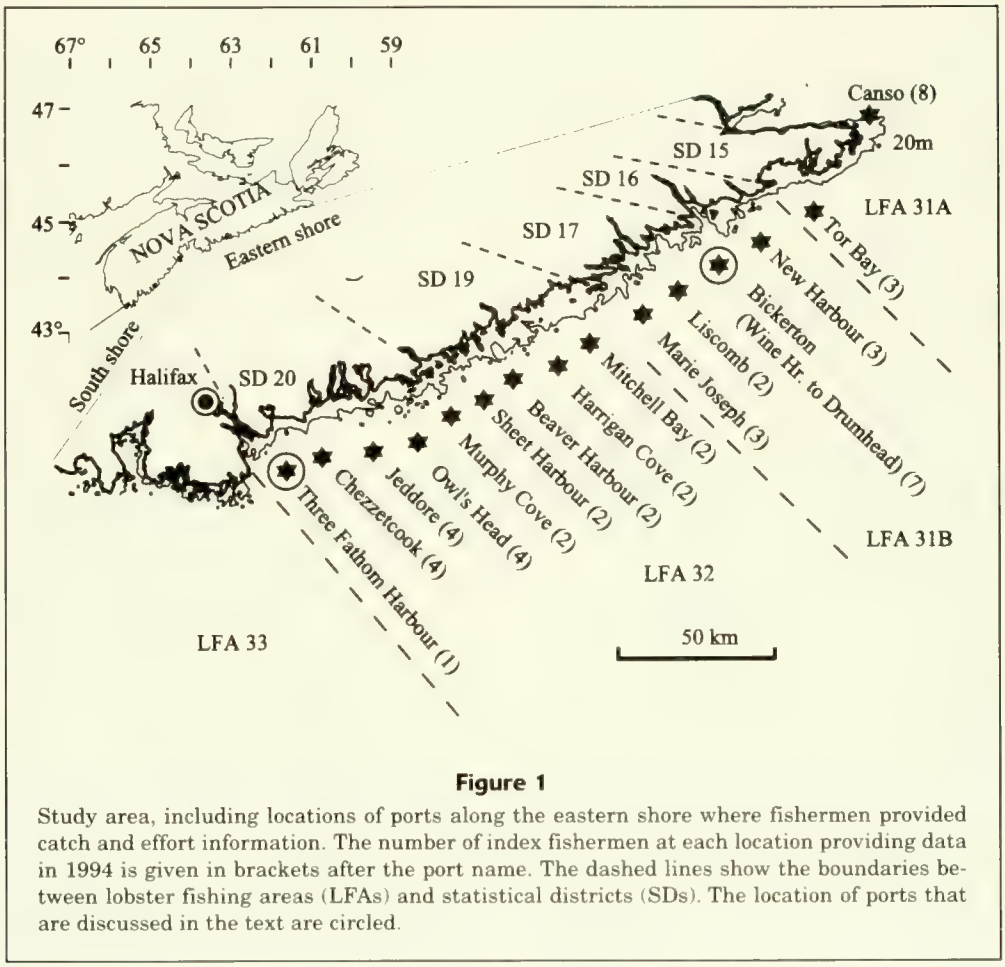

Figure 1

Study area, including locations of ports along the eastern shore where fishermen provided catch and effort information. The number of index fishermen at each location providing data in 1994 is given in brackets after the port name. The dashed lines show the boundaries between lobster fishing areas (LFAs) and statistical districts (SDs). The location of ports that are discussed in the text are circled.

Materials and methods

Annual lobster catch is recorded by statistical district from purchase slips by the Department of Fisheries and Oceans (DFO). These data are summarized by larger geographical units for assessment purposes, usually by lobster fishing areas (LFAs). In order to examine the large scale relationships between catches and temperature, catches were summarized in a similar manner for this analysis. The Atlantic coast of Nova Scotia (Fig. 1) was bisected into coastlines of approximately equal length, named the eastern shore (LFAs 31A, 31B, and 32) and south shore (LFA 33). Long-term records of sea surface temperatures (SSTs) are available from Halifax harbour which is located on the boundary between these areas and can be considered representative of both.

The three data series, i.e. total annual catches from the south and eastern shore and average annual SSTs, were smoothed with a 3-yr running average. Examination of the plots suggested that the series could be divided into two periods, a pre-1974 period of high-frequency, low-amplitude cycles, and a single post-1974 cycle of high amplitude. Correlations at lags of 0–10 years were then run for each period separately and combined.

Daily catch and effort information is collected for DFO by selected index fishermen in some areas of Nova Scotia. At minimum these fishermen provide total lobster catches (usually weight in pounds) and the number of traps hauled on a daily basis during the fishing season. The number of index fishermen varies between areas but tends to cluster around key ports that are also sampled for length frequencies by port samplers. On the eastern shore, about 20 fishermen have kept log books along a 200-km stretch of coastline between Canso and Halifax, some beginning as early as 1986. In 1994 an additional 28 fishermen associated with the Fishermen's and Scientists' Research Society (FSRS) kept logs in this area. Most FSRS fishermen also deployed continuous temperature recorders (Vemco Ltd., Halifax, N.S.) on their traps during the 1994 fishing season, which extended from 20 April to 20 June in LFAs 31B and 32, and from 1 May to 31 June in LFA 31A. Because effort information is available only for a limited num-

Table 1

Statistics for correlation analysis of data series in Figure 1.

	Eastern shore			South shore		
	significant lags (yr)	lag (yr) at maximum r	r	significant lags (yr)	lag (yr) at maximun r	r
Pre-1974	1–3	2	0.683*	0–2	1	0.688*
Post-1974	—	8	0.519	—	6	0.532

* = significant at $P<0.01$

ber of index fishermen within each statistical district, total effort for each district was calculated by dividing its total catch by the average catch per trap haul (CPTH) for index fishermen in that district.

Because seasonal trends were evident in temperature, CPTH, and effort data, any analysis involving daily observations of these parameters were detrended by using first differencing i.e. $i - (i - 1)$, where i is the individual observation of temperature, CPTH, or catch. This avoided spurious negative correlations between the decreasing catches throughout the season that were due to depletion of the fishable biomas, and increasing spring–summer temperatures. Because most fishermen on the eastern shore attempt to haul their traps daily and because longer soaks are usually associated with unfavorable weather (which tends to affect most fishermen in the same area), there was no attempt to adjust for differences in soak times within or between each fisherman's time series. Inspection of the data showed that gaps in the individual time series tended to occur on the same days, which coincided with storm days and Sundays.

Temperature information was also available from DFO moored recorders moored along the eastern shore during the period when logbooks were kept. Years with a strong association between temperature and catch were identified for further study at smaller spatial and temporal scales as follows: daily, temperature, catch, and effort data from the 1986–94 fishing seasons at the location with the most complete longer-term records, i.e. Port Bickerton, were detrended as described above and the resulting individual series correlated. This analysis identified 1991 and 1994 as years with significant correlations. The latter year was chosen for further investigation into the nature of this relationship because of the availability of data at small spatial scales throughout the area from FSRS records. Three matrices of port versus date, one each for the detrended temperature, CPTH and effort data, were then developed for further correlation analysis. Each matrix resulted in a port versus port matrix of correlation coefficients, i.e indices of similarity between port pairs in terms of the daily patterns of change for the respective parameters. Correlations between port pairs could then be plotted against distance between them.

Results and discussion

Effort information is not available at the largest spatial and longest temporal scale examined (Atlantic coast of Nova Scotia, 50 years). At this scale, however, there is a significant correlation between annual mean sea surface temperatures in the approximate center of the area (i.e. Halifax harbor) and summarized lobster catches (Fig. 2; Table 1) at short lags prior to 1974. This correlation was also noted by Campbell et al (1991). Catches are significantly correlated ($P<0.01$) with temperatures for three cycles prior to 1974 at lags of 1–3 years on the eastern shore and 0–2 years on the south shore. After 1974, correlations are highest (although marginally insignificant) at lags of 8 years on the eastern shore and 6 years on the south shore, approximately the time lobsters take to recruit to the fishery in these areas. This finding suggests that during this period, temperature or an unknown covariate also influenced the survival of larvae and subsequently increased recruitment to the fishery. The increase in catches in both areas after 1974 is consistent with the northwest Atlantic coast-wide "recruitment pulse" (Pezzack 1992), which is generally attributed to a common environmental influence, although Drinkwater et al (1996) concluded that this environmental influence was not temperature. Prior to 1974 the near in-phase changes in temperature and catch along the eastern and south shore could be due to temperature-induced changes in catchability during warmer years i.e. to greater activity of lobsters on the grounds or faster growth to legal size, or to both. However, without long-term effort information, changes in effort cannot be

ruled out as a cause of the pre-1974 catch cycles. For example, because Halifax harbour sea surface temperatures reflect weather conditions in the study area, years with colder sea surface temperatures could also be years with less fishing activity. It is noteworthy that along the eastern shore both pre- and post-1974 catches lag temperatures by 1–2 yr longer than on the south shore. Hudon (1994) noted that the population along the eastern shore may be growth-limited owing to colder water temperatures than those in adjacent areas, and one would expect this area to react more slowly to the more moderate temperature increases.

Catch and effort in smaller statistical districts along the eastern shore, along with available temperature indices in the area (Fig. 3), reflect the catch patterns of most other lobster fishermen in the northwest Atlantic during this period, i.e. peak catches in the late 1980s and subsequent declines. There was an increase in effort along the eastern shore throughout the period. There is no apparent relation between catches and available temperature indices, although the warmest water and highest catch both occurred in the same year (1989).

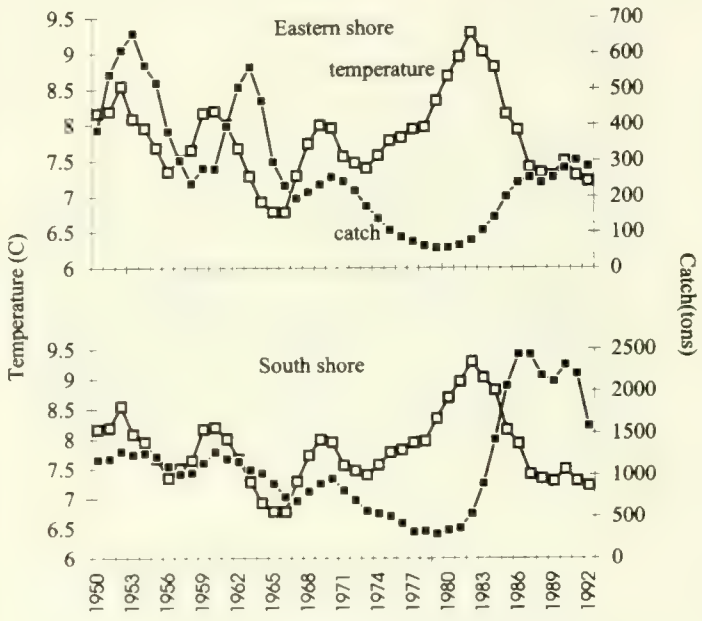

Figure 2

Total annual lobster catch for the eastern shore and south shore of Nova Scotia and average annual sea surface temperatures in Halifax harbor, 1950–92. All data series were smoothed with a three year average.

Port Bickerton reflected the catch and effort pattern of the eastern shore as a whole, including an increase in effort throughout most of the period (Fig. 4). Note that the increase in the average daily number of trap hauls leveled off when catches started to decline after 1991. Perhaps fishermen were increasing effort in response to increasing lobster catches during the 80s. Pringle and Duggan (1984) noted that as many as 25% of the maximum number of traps (eastern shore trap limit is 250) can remain unused in the Nova Scotia lobster fishery. Although the use of catches alone would have overestimated the rate of increase in the population during the 80s and underestimated the subsequent decline, the differences are small and would not have affected conclusions on annual population changes.

A significant correlation between average daily temperatures and CPTH at Port Bickerton occurred in only 2 of the 8 years for which temperature, catch, and effort information is available at this scale, suggesting that short-term, temperature-induced changes in catchability occurred, or were detectable, during those years (Tables 2 and 3). However, a multiple regression of daily catch (dependent variable) versus effort and temperature during these years also indicates that short-term changes in lobster catches were largely determined by effort changes. Cross correlations between total daily catch and effort at Port Bickerton at lags of 0–7 days showed no significant correlations at lags other than 0, indicating that fishermen's effort was not influenced by catches at short time scales.

Table 2

Pearson correlation coefficients for average daily temperature (at 10 m) vs. total daily catch, total daily effort, and average daily catch per trap haul for index fishermen at Port Bickerton 1986–94.

	Catch	Effort (trap hauls)	Average CPTH
1986	0.0491	0.1066	0.0830
1987	0.2158	0.0065	0.1740
1988	–0.0380	–0.0373	0.1060
1989	–0.0551	0.0718	0.1580
1990	0.1317	0.1239	0.1690
1991	0.311*	0.1014	0.408*
1992	–0.1426	–0.2853	0.2110
1993[1]			
1994	0.2477	0.1888	0.262*

* = significant at $P<0.05$

[1] Temperature data for 1993 were not available in Bickerton during the fishing season.

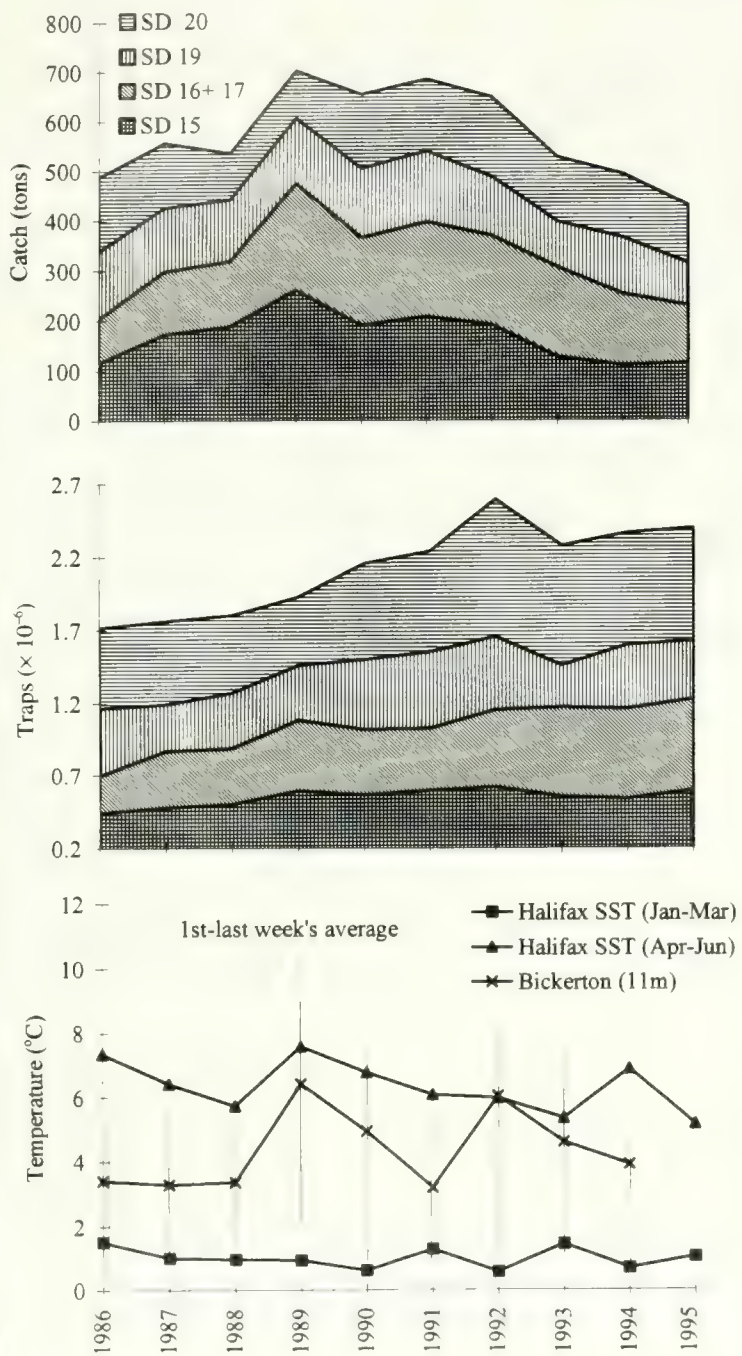

Figure 3

Total annual lobster catch (top) and total annual effort (middle) for eastern shore statistical districts from 1986–95, the years for which effort information is available from index fishermen. Also shown for these years are three temperature indices (bottom), including average sea surface temperatures (SST) in Halifax harbour from January to March; average SST from April to June i.e. during the lobster season; and average water temperatures (11 m) at Port Bickerton during the lobster season. The bars show the average temperature for the first (lower) and last (upper) week of the lobster season.

Correlation coefficients of the daily first differenced CPTH data from individual fishermen on the eastern shore were plotted against distance from Port Bickerton and Three Fathom Harbour (Fig. 5), situated about 125 km apart near the northeastern and southwestern end of the study area (Fig. 1). Correlations were strongest in the immediate vicinity of these ports, decreased to insignificance at about 50 km, then increased to a second maximum at 125 km. This pattern was still apparent when all ports were included in the analysis (Fig. 5, bottom), but the least-squares fit to the polynomial was not as good, perhaps because local factors influence the main spatial trend in other areas. In contrast, short-term changes in water temperature are strongly correlated throughout the area (Fig. 6) because they are caused by wind events that impact the eastern shore as a whole. Apparently, the correlation of catches and temperatures at Port Bickerton in 1994 (Table 2) occurred only at either end of the eastern shore. To determine if this correlation was truly a direct environmental influence on catch, I plotted the daily correlation coefficients of all ports against distance separately for CPTH and effort (Fig. 7). The fourth-order polynomials fitted to the data are similar for both, indicating that the similarity in catches between ports on either end of the eastern shore and their similarity to short-term temperature changes are mainly due to similarities in the daily pattern of change in effort. This is confirmed by plotting the coefficients for effort versus temperature directly. Similar results were obtained for 1991, the other year in which significant correlations between temperature and catches were found at Port Bickerton. The reason why fishermen separated by 125 km have similar day-to-day fishing patterns is apparent when one examines the nature of the coastline along the eastern shore (Fig. 1). The coast near Three-Fathom Harbour and Bickerton is characterized by relatively long and narrow bays generally oriented in a north–south direction, which offer more shelter than the relatively exposed coastline between them. If the winds that cause temperature decreases are also those that make fishing more difficult,

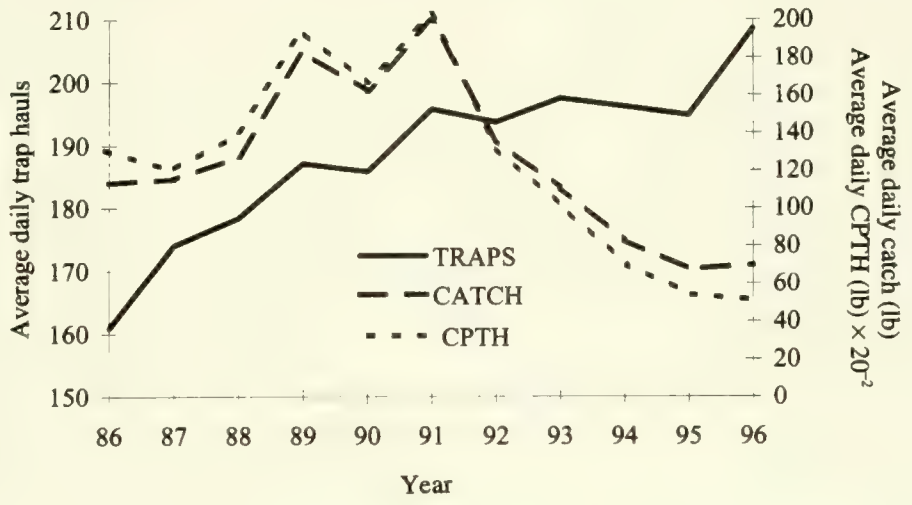

Figure 4

Annual averages of daily catch, trap hauls, and catch per trap haul for index fishermen at Port Bickerton 1986–96.

Table 3

Multiple regression analysis of total daily catch (dependant variable), total daily effort (trap hauls) and average daily temperatures for the two years where significant correlations between temperature and catch per trap haul were found (Table 1). Statistics shown include slope and intercept values (B), standard error of B, and regression coefficients (Beta), with their significance levels (Sig. T).

		B	SE B	Beta	T	Sig. T
1991	Effort	1.1382	0.1055	0.8241	10.7840	0.0000
	Temperature	50.9725	62.0185	0.0628	0.8220	0.4148
	(Constant)	–0.9795	34.8649	–0.0280	0.9777	
1994	Effort	0.4000	0.0528	0.7179	7.5760	0.0000
	Temperature	61.3956	51.8943	0.1121	1.1830	0.2423
	(Constant)	–10.4788	28.9416	–0.3620	0.7188	

e.g. those that are southerly and enter directly into the bays, and are of a minimum force, or both, one would expect a positive correlation between water temperatures and catches in these areas. The apparently spurious correlation between lobster catches and temperature would be weaker in the exposed central area where fishing activity is vulnerable to winds from a wider direction and of less force than those which significantly impact near-shore water temperatures. Although it is clear that the observed correlations between short-term changes in lobster catches and temperatures are strongly influenced by changes in effort, these results do not rule out a concurrent direct affect of temperature on lobster activity and catches, i.e. effect of catchability. Possibly fishermen are aware that winds of a certain direction and force affect lobster activity and catchability and alter their fishing activity accordingly, or the factors that decrease fishing activity also decrease lobster catchability independently.

These results indicate that although changes in effort can influence lobster catches at all spatial and temporal scales examined, data on effort is particularly critical in correctly interpretating the meaning of changes in catch at smaller scales i.e. <100 km and <1 yr. In particular, they indicate that small-scale correlations between environmental parameters such as winds and water temperatures with lobster catches alone should be treated cautiously because inferences made about their underlying mechanisms may be wrong. For example, Hudon (1994) concluded that differences in annual catches between approximately 100-km lengths of the Nova Scotia coastline were due to differences in the orientation of these coastlines to upwelling winds, the resultant change in wa-

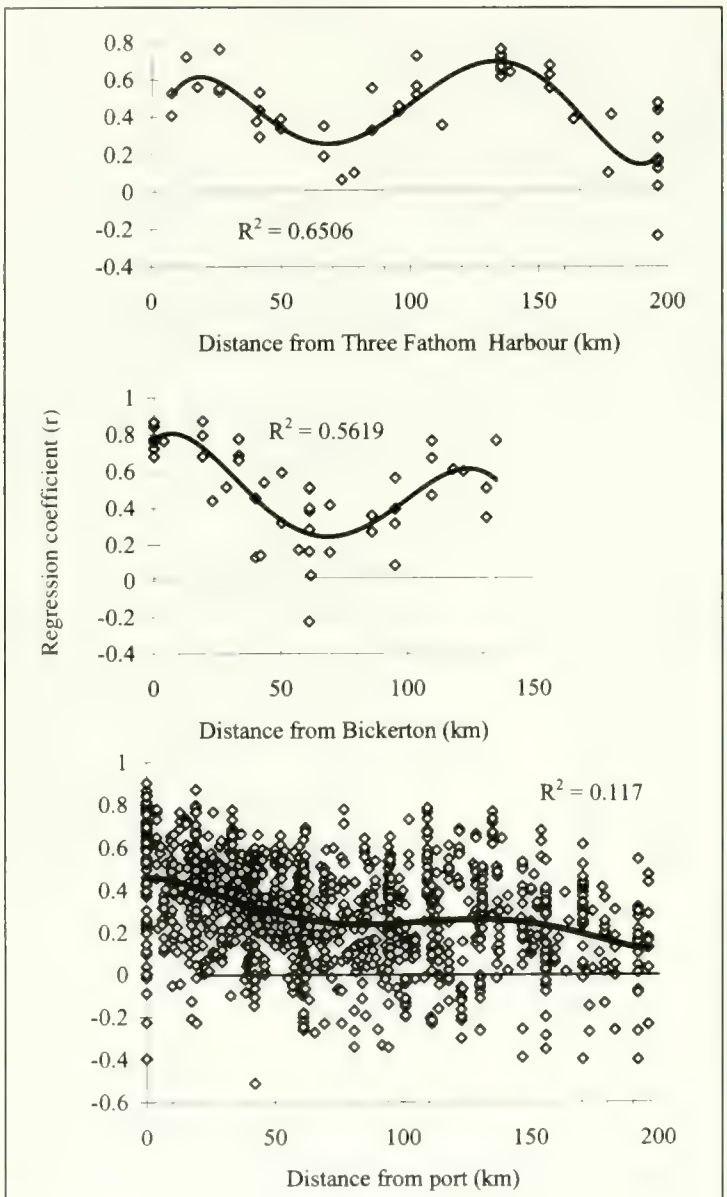

Figure 5

Pearson correlation coefficients of first differenced daily CPTH of all index fishermen along the eastern shore versus increasing distance from Three Fathom Harbour (top) and Bickerton (middle). The bottom figure plots the same statistic for all ports versus distance from each other. A fourth order polynomial provided the best least-squares fit to each data set.

ter temperature, and the effect of the latter on lobster productivity. This study suggests that at least some of these differences may be due to differences in effort and "fishability" of the coastlines involved.

These results also give a general indication of the sampling effort (i.e. number of index fishermen) and distribution (spacing of index fishermen) required of a program whose objective is to characterize and assess changes in effort for an entire coastline. Because changes in effort from index fishermen separated by short distances, i.e. within the working reaches of a fishing port, are strongly correlated, it would be more effective for any given total sampling intensity to space samples evenly along that coastline, rather than cluster them in ports. Since the correlation of index fishermen's catch data decreases quickly at dis-

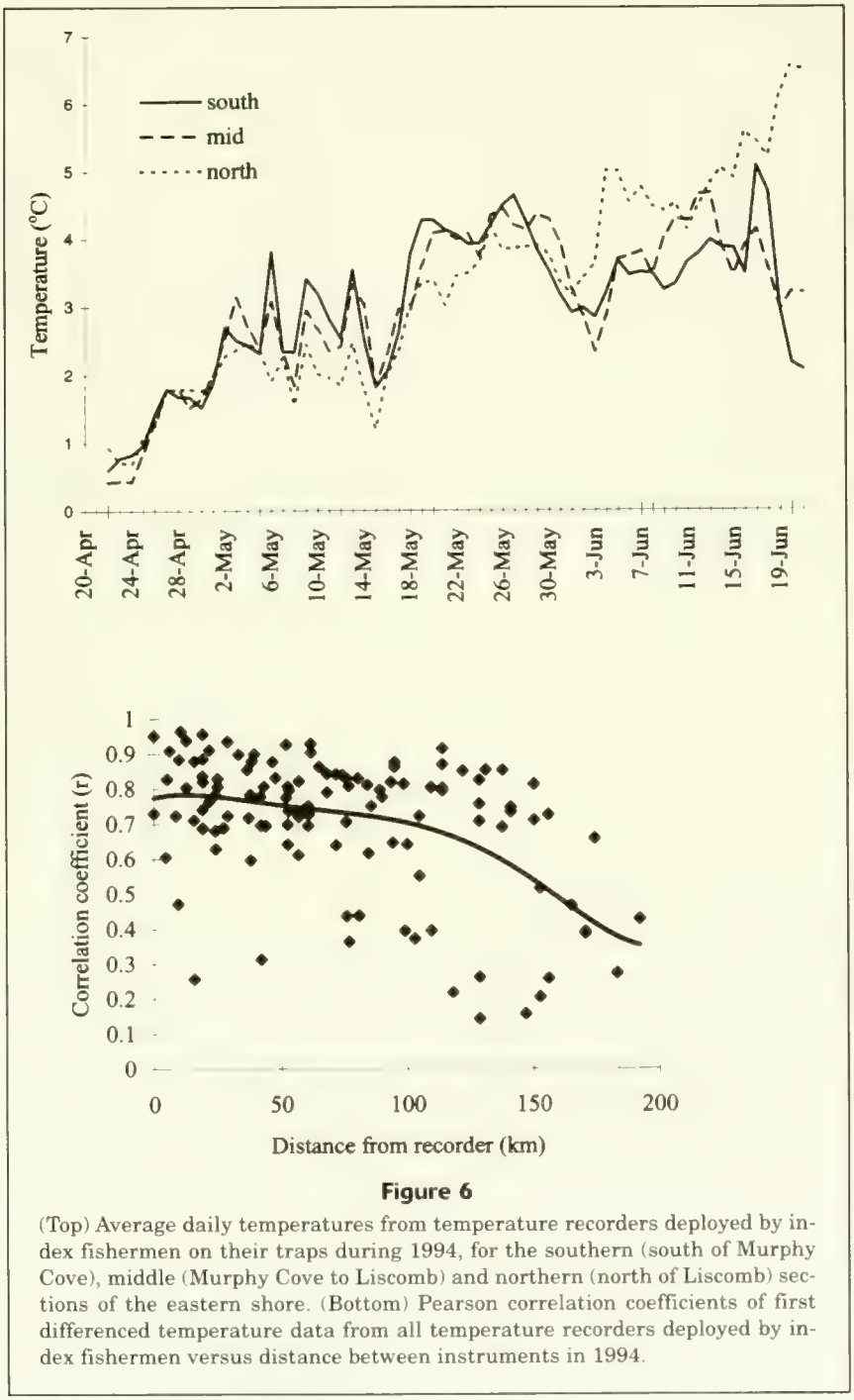

Figure 6

(Top) Average daily temperatures from temperature recorders deployed by index fishermen on their traps during 1994, for the southern (south of Murphy Cove), middle (Murphy Cove to Liscomb) and northern (north of Liscomb) sections of the eastern shore. (Bottom) Pearson correlation coefficients of first differenced temperature data from all temperature recorders deployed by index fishermen versus distance between instruments in 1994.

tances greater than about 25 km, the samples should be more closely spaced. On the eastern shore, where the annual average number of fishermen providing information is about 20, the resulting 10-km spacing at this sampling level should be adequate to provide a representative sample.

Although these results have not eliminated the possibility of temperature-induced changes in catchability, they do indicate that quantifying these changes with fishermen's data would be extremely difficult.

Acknowledgments

I wish to thank the Nova Scotia lobster fishermen who provided information used in this study, especially those who have collected data since the begin-

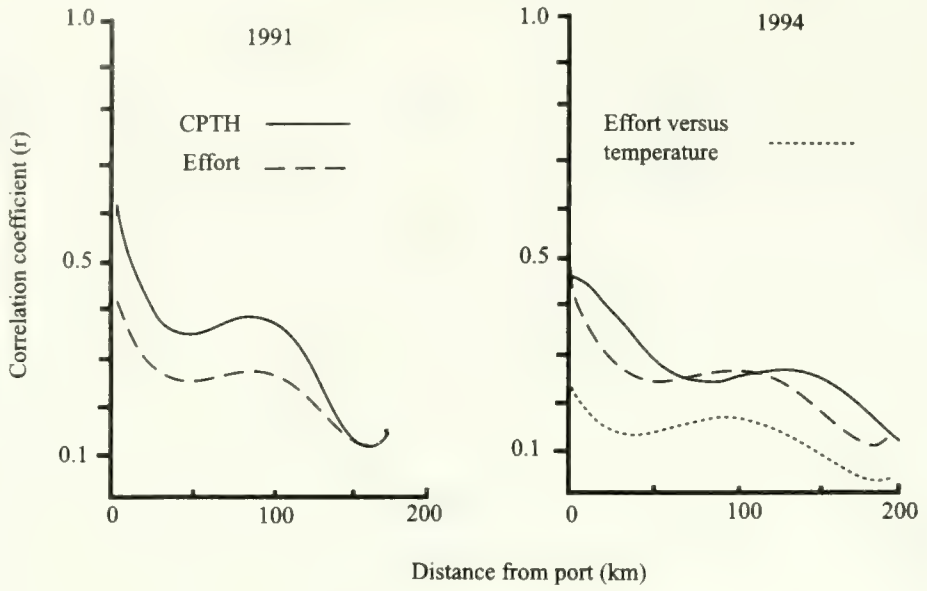

Figure 7

Fourth order polynomials as shown in the bottom of Figure 5, but for catch per trap haul and trap hauls separately, for the years in which significant correlations of daily temperature and catch per trap haul were found at Port Bickerton (1991, 1994). Also shown is the polynomial curve for individual fishermen's daily effort versus daily average temperatures in their area in 1994. Individual points have been omitted for clarity, but their distribution is similar to the bottom of Figure 5.

ning of DFO's lobster logbook program. Their continuing efforts increase the value of this database each year. The cooperation of Randy Baker, Sean Smith, and fishermen of the Fishermen's and Scientists' Research Society is gratefully acknowledged for access to additional data for the 1994 season, including temperatures. Ed Verge provided historical temperature data collected by the Physical and Chemical Sciences Branch, DFO, and Ron Duggan summarized much of the data for analysis. Bob Roger and Steve Smith provided statistical advice, and John Tremblay and Doug Pezzack reviewed early versions. I am particularly indebted to three anonymous reviewers whose suggestions significantly improved the manuscript.

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Abstract.—We evaluated the use of total body electrical conductivity (TOBEC) for determination of whole-body water content of yellow perch, *Perca flavescens*, and alewife, *Alosa pseudoharengus*. We used multiple linear regression with backwards stepwise elimination to test the capability of TOBEC values, wet weight, and total length in predicting whole-body water content of yellow perch and alewife. We found that wet weight was the best predictor of whole-body water content. The inclusion of TOBEC values in multiple linear regressions did not improve the predictive capability of wet weight over simple linear regressions that used wet weight alone (r^2 increased by only 0.00002 to 0.0005). We reanalyzed the data from three previous studies that used TOBEC to evaluate the tissue composition of fish. Again we found that the inclusion of TOBEC values in regression functions with wet weight as the other independent variable did not substantially improve the predictive capability of functions that used wet weight alone (r^2 increased by only 0.00003 to 0.0007).

Evaluation of total-body electrical conductivity to estimate whole-body water content of yellow perch, *Perca flavescens*, and alewife, *Alosa pseudoharengus**

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Attempts to construct energy budgets for many important fish species are often hampered by the lack of data on their energy density. Further, the study of energy flow in aquatic communities is complicated by seasonal variation of the energy density within organisms and relative differences in energy content of predator and prey (Craig, 1977; Stewart et al., 1983; Stewart and Binkowski, 1986; Rand et al., 1994). The shortage of useful data is due in part to the difficulty of determining the energy content of large numbers of individuals. Estimation of fish energy density has been simplified with development of relationships, based on calorimetric analysis, between percentage dry weight ($100 \times$ (dry weight/wet weight)) and wet weight energy density (Stewart and Binkowski, 1986; Rand et al., 1994; Hartman and Brandt, 1995; Lantry, 1997). The measurement of dry weights on substantial numbers of large individual fish, however, can be problematic, because they require considerable time to dry, use large amounts of oven space, and may require time-consuming sectioning or grinding procedures.

Measurement of total body electrical conductivity (TOBEC) has been presented in the literature as a reliable alternative to the sacrifice of organisms to evaluate tissue composition. Lipid content and lean body mass have been accurately estimated by measuring TOBEC in humans, swine, rats and birds (Domermuth et al., 1976; Bracco et al., 1983; Presta et al. 1983; Keim et al., 1988; Walsberg, 1988; Castro et al., 1990). TOBEC has recently been used for the estimation of body composition of three fish species: sunshine bass (a white bass [*Morone chrysops*] × striped bass [*Morone saxatilis*] hybrid, Brown et al., 1993); red drum (*Sciaenops ocellatus*, Bai et al., 1994); and channel catfish (*Ictalurus punctatus*, Jaramillo et al., 1994).

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In our analyses of fish community dynamics in Lake Ontario and Oneida Lake, New York, we used bioenergetics to evaluate trophic transfer and tissue growth (Rand et al., 1995; Lantry, 1997). To model trophic energy flux accurately, we needed to estimate fish energy content throughout the years being simulated. Because of the difficulty encountered in drying large numbers of fish and in drying large individuals, we sought an alternative method—measurement of whole-body water content. Our objective here was to evaluate the use of TOBEC as an alternative to drying, for estimating the whole-body water content of yellow perch (*Perca flavescens*), an important prey and sport fish component of both lakes, and alewife (*Alosa pseudoharengus*), the dominant planktivore and prey fish in Lake Ontario.

Materials and methods

We used the "EM-SCAN Inc. SA2 Small Research Animal Body Composition Analyzer" to obtain TOBEC values for yellow perch and alewife. The measurement principle of the EM-SCAN has been published elsewhere (Fiorotto et al., 1987; Walsberg, 1988; Brown et al., 1993). The scanner uses a radiating coil to set up a low-frequency electromagnetic field to measure the electrical conductivity of an animal. Because electricity is conducted by the ions dissolved in body water, the most direct relationship that can be drawn from the TOBEC values is the amount of water contained within an animal. By initially measuring the wet weight of a fish and then measuring the whole-body water content with the scanner, we could obtain the dry weight of the fish by difference, and calculate the percentage dry weight, which is the key parameter we needed to estimate energy density.

Sample collection and processing

We collected 43 yellow perch in bottom trawls from Oneida Lake, NY, over four dates in 1992: 23 April, n=10; 9 June, n=5; 30 September, n=10; and 23 November, n=18. We collected 47 alewife from the New York waters of Lake Ontario with a 3-m bag seine on 2 May (n=13) and 4–5 July (n=34) 1993. Yellow perch were kept alive in lake water during sampling, and alewife were placed on ice immediately after capture. All fish were frozen in water upon arrival at the laboratory.

During processing, fish were thawed under warm running water, blotted dry, weighed to the nearest 0.1 g and measured for total length (mm). We obtained TOBEC values according to the procedures outlined in the scanner manual (EM-SCAN Inc., 1991). Because the positioning of the animal is important in obtaining consistent conductivity readings, fish were placed on their right sides headfirst on the animal carrier trays with the portion of their bodies anterior to the distal end of the shortest ray of the pelvic fin lined up in front of the scribed mark on the tray. Each fish was scanned five times in the scanner's fixed mode and the readings were averaged to produce a mean TOBEC value. After scanning, all fish were dried to a constant weight at 65°C.

Statistical analysis

We constructed simple and multiple linear regression models to predict whole-body water content (*WC*, g). Following earlier fish studies (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994) we included wet weight (*WWT*, g), total length (*TL*, mm), and *TOBEC* as independent variables in regressions. We graphed these variables against fish *WC* (determined from drying individuals) to evaluate the shape of the relationships. We transformed independent variables when relationships with *WC* departed from linear trends. We used SYSTAT 5.03 for Windows (1993) to perform stepwise multiple linear regressions with backwards elimination on all variables (inclusion probability: $P \geq 0.15$) to determine which independent variables accounted for most of the variation in predictive equations (Zar, 1984; Neter et al., 1985). The resulting regression models were then used to predict *WC* and calculate percentage error (*PE*):

$$PE = \left\{\left(\left|\text{actual} - \text{predicted}\right| / \text{actual}\right) \times 100\right\}.$$

Finally, we calculated percentage dry weight from both actual (determined from drying) and predicted (from regression equations) water content and compared the variation between these values to the range of percentage dry weights commonly observed for yellow perch and alewife (Tables 1 and 2).

Results

Significant (P<0.05) positive relationships were found in simple linear regressions between the dependent variable *WC* and the independent variables *TOBEC*, *WWT*, and *TL* for both yellow perch and alewife (r^2=0.66 to 0.99). Simple linear regressions of *TOBEC* on *WC* produced r^2 values of 0.933 and 0.667 for yellow perch and alewife, respectively. Multiple linear regressions with two independent variables (*WWT* and *TOBEC*) gave excellent fits to the data for both species. The equation for yellow perch was

$$WC = 3.46239 + 0.69844 \times WWT + 0.00559 \times TOBEC \quad (r^2=0.998).$$

Table 1

Yellow perch individual water content (g) from measurements (act) and predicted (pred) from regression functions. TOBEC is the average scanner conductivity index (based on five consecutive measurements). %DWT is the percentage dry weight and is equivalent to: {(|wet weight – water|)/wet weight} × 100. Values in parentheses are percentage errors (PEs) referring to water (g) and %DWT, and are equivalent to {(|actual – predicted|)/actual} × 100.

Total length (mm)	Wet weight (g)	TOBEC	Water (g) (act)	Water[1] (g) (pred)		Water[2] (g) (pred)		%DWT (act)	%DWT[1] (pred)		%DWT[2] (pred)	
196	99.5	138.6	76.8	73.73	(3.99)	76.02	(1.01)	22.81	25.90	(13.51)	23.59	(3.42)
166	66.5	65.6	50.8	50.28	(1.03)	51.30	(0.98)	23.61	24.40	(3.34)	22.86	(3.15)
148	51.0	42.6	39.2	39.32	(0.31)	39.83	(1.61)	23.14	22.90	(1.03)	21.90	(5.36)
157	51.2	40.4	39.2	39.45	(0.63)	39.79	(1.50)	23.44	22.95	(2.07)	22.29	(4.91)
160	57.1	48.8	44.0	43.62	(0.87)	44.18	(0.42)	22.94	23.61	(2.93)	22.62	(1.40)
151	46.8	28.2	35.6	36.31	(1.99)	35.94	(0.95)	23.93	22.42	(6.31)	23.21	(3.02)
137	31.4	17.6	25.2	25.49	(1.16)	25.00	(0.81)	19.75	18.82	(4.71)	20.40	(3.31)
141	35.0	20.8	27.2	28.02	(3.03)	27.66	(1.68)	22.29	19.93	(10.57)	20.98	(5.86)
133	27.9	12.8	21.7	23.02	(6.08)	22.14	(2.05)	22.22	17.49	(21.30)	20.63	(7.12)
135	29.7	14.6	23.3	24.29	(4.24)	23.54	(1.02)	21.55	18.22	(15.43)	20.75	(3.70)
239	223.1	346.6	154.7	161.22	(4.20)	161.76	(4.54)	30.64	27.73	(9.49)	27.49	(10.28)
275	288.6	481.9	199.8	207.73	(3.96)	206.90	(3.55)	30.76	28.02	(8.92)	28.31	(7.99)
265	296.6	466.8	204.2	213.23	(4.43)	211.67	(3.66)	31.16	28.11	(9.79)	28.64	(8.09)
271	290.3	415.9	203.4	208.55	(2.54)	206.44	(1.51)	29.94	28.16	(5.95)	28.89	(3.52)
229	210.9	361.5	151.4	152.79	(0.88)	154.37	(1.93)	28.19	27.56	(2.25)	26.81	(4.91)
242	284.6	642.5	204.6	205.83	(0.57)	207.73	(1.51)	28.10	27.68	(1.50)	27.01	(3.88)
258	301.5	586.0	217.5	217.32	(0.09)	217.39	(0.06)	27.86	27.92	(0.23)	27.90	(0.15)
256	260.2	538.4	198.2	188.21	(5.03)	190.02	(4.12)	23.84	27.67	(16.08)	26.97	(13.16)
261	280.0	561.7	210.9	202.17	(4.12)	203.15	(3.65)	24.69	27.80	(12.57)	27.44	(11.15)
201	106.2	108.3	82.1	78.24	(4.64)	78.94	(3.79)	22.74	26.33	(15.78)	25.67	(12.89)
195	101.1	96.8	77.3	74.62	(3.50)	75.12	(2.85)	23.51	26.20	(11.40)	25.70	(9.28)
209	132.9	155.2	100.4	97.15	(3.20)	98.03	(2.32)	24.48	26.90	(9.88)	26.24	(7.17)
205	139.6	179.1	107.4	101.97	(5.04)	103.23	(3.86)	23.08	26.96	(16.80)	26.05	(12.87)
163	54.6	36.2	39.1	41.80	(6.82)	41.62	(6.37)	28.33	23.44	(17.26)	23.77	(16.11)
144	41.8	24.2	31.8	32.79	(3.11)	32.36	(1.74)	23.91	21.55	(9.88)	24.34	(5.88)
156	45.4	26.8	34.5	35.32	(2.37)	34.91	(1.18)	24.00	22.20	(7.51)	23.10	(3.75)
147	40.6	22.1	31.2	31.94	(2.44)	31.37	(0.61)	23.20	21.32	(8.08)	22.73	(2.03)
131	27.9	11.0	21.6	23.01	(6.34)	21.88	(1.14)	22.44	17.53	(21.90)	21.56	(3.92)
128	26.4	10.8	20.6	21.96	(6.42)	20.90	(1.26)	21.83	16.81	(22.99)	20.84	(4.52)
116	17.6	5.8	13.8	15.79	(14.35)	14.40	(4.32)	21.55	10.30	(52.22)	18.16	(15.74)
127	23.7	10.0	18.8	20.07	(6.64)	19.05	(1.21)	20.59	15.31	(25.62)	19.62	(4.68)
129	25.7	11.2	20.4	21.48	(5.30)	20.51	(0.57)	20.64	16.44	(20.37)	20.19	(2.18)
224	172.2	222.2	130.7	124.99	(4.37)	125.58	(3.93)	24.10	27.42	(13.77)	27.08	(12.36)
215	138.4	156.3	105.8	100.97	(4.60)	101.56	(4.04)	23.50	27.02	(14.97)	26.60	(13.15)
281	285.9	378.8	211.9	205.24	(3.13)	202.67	(4.34)	25.88	28.20	(8.96)	29.10	(12.42)
294	387.6	818.4	281.3	278.74	(0.92)	276.73	(1.63)	27.42	28.08	(2.43)	28.60	(4.32)
173	83.0	79.2	62.0	61.90	(0.11)	62.65	(1.10)	25.37	25.45	(0.34)	24.55	(3.22)
227	183.4	273.3	130.6	133.11	(1.94)	134.36	(2.89)	28.81	27.43	(4.79)	26.76	(7.15)
240	237.5	407.6	167.4	171.60	(2.49)	172.50	(3.03)	29.49	27.74	(5.95)	27.36	(7.25)
272	295.5	592.5	215.6	213.10	(1.16)	213.67	(0.91)	27.02	27.86	(3.12)	27.68	(2.47)
278	333.7	784.7	233.4	240.89	(3.23)	241.71	(3.58)	30.06	27.80	(7.52)	27.56	(8.33)
339	434.2	1165	314.3	313.26	(0.32)	312.02	(0.71)	27.63	27.86	(0.83)	28.14	(1.86)
Mean PE's					(3.33)		(2.23)			(10.60)		(6.59)

[1] Predicted (pred) values from the regression function with wet weight (g) and TOBEC as the independent variables.
[2] Predicted (pred) values from the regression function with wet weight (g) and square root transformed scanner conductivity index as the independent variables.

Table 2

Alewife individual water content (g) from measurements (act) and predicted (pred) from regression functions. TOBEC is the average scanner conductivity index (based on five consecutive measurements). %DWT is the percentage dry weight and is equivalent to {(|wet weight − water|)/wet weight} × 100. Values in parentheses are percentage errors (PEs) referring to water (g) and %DWT and are equivalent to {(|actual − predicted|)/actual} × 100. Predicted (pred) values are from the regression function with wet weight (g) and TOBEC as the independent variables.

Total length (mm)	Wet weight (g)	TOBEC	Water (g) (act)	Water (g) (pred)		%DWT (act)	%DWT (pred)	
153	22.85	11.0	18.24	18.70	(2.49)	20.15	18.16	(9.88)
158	27.68	17.0	22.25	22.53	(1.25)	19.62	18.61	(5.14)
166	28.11	14.2	23.69	23.02	(2.83)	15.73	18.12	(15.17)
160	27.02	12.2	21.65	22.18	(2.45)	19.87	17.91	(9.87)
163	29.08	17.4	23.77	23.69	(0.33)	18.24	18.51	(1.50)
164	27.92	13.4	22.29	22.89	(2.72)	20.18	18.01	(10.74)
163	30.41	17.4	23.18	24.82	(7.10)	23.78	18.37	(22.75)
149	22.83	10.6	19.09	18.70	(2.04)	16.38	18.08	(10.42)
163	28.92	15.8	23.99	23.63	(1.48)	17.06	18.28	(7.18)
156	24.91	15.0	20.47	20.27	(0.96)	17.83	18.62	(4.45)
142	20.87	13.8	16.51	16.90	(2.36)	20.89	19.02	(8.95)
155	22.86	12.2	18.93	18.66	(1.42)	17.21	18.39	(6.81)
156	21.14	10.2	17.58	17.29	(1.64)	16.86	18.22	(8.07)
186	41.05	19.6	33.78	33.74	(0.11)	17.71	17.81	(0.53)
183	47.84	26.6	37.94	39.19	(3.29)	20.70	18.09	(12.60)
168	37.97	17.0	30.58	31.25	(2.20)	19.48	17.71	(9.08)
178	40.16	23.2	33.42	32.83	(1.76)	16.79	18.25	(8.70)
171	31.80	13.8	26.25	26.16	(0.33)	17.46	17.74	(1.56)
168	31.88	13.6	26.81	26.23	(2.17)	15.88	17.70	(11.48)
166	32.07	15.4	25.90	26.32	(1.63)	19.25	17.93	(6.85)
166	32.49	12.2	26.94	26.81	(0.47)	17.08	17.47	(2.29)
158	32.83	13.8	27.62	27.04	(2.12)	15.87	17.66	(11.25)
174	40.39	20.4	33.58	33.15	(1.29)	16.86	17.93	(6.36)
148	27.02	11.4	21.71	22.21	(2.34)	19.66	17.78	(9.55)
160	34.66	14.6	27.41	28.55	(4.16)	20.92	17.64	(15.71)
176	32.51	11.8	27.31	26.85	(1.69)	15.99	17.41	(8.89)
175	37.82	16.8	31.31	31.13	(0.58)	17.21	17.70	(2.80)
159	27.34	13.6	22.81	22.39	(1.85)	16.56	18.10	(9.35)
166	40.33	16.6	33.16	33.26	(0.30)	17.77	17.52	(1.39)
171	37.15	16.0	30.78	30.60	(0.59)	17.16	17.64	(2.83)
172	37.97	21.6	31.04	31.04	(0.00)	18.24	18.24	(0.02)
162	32.89	16.0	26.38	26.99	(2.31)	19.80	17.95	(9.34)
180	44.45	21.0	36.61	36.56	(0.12)	17.65	17.75	(0.55)
170	37.20	16.2	29.65	30.63	(3.30)	20.29	17.66	(12.95)
177	39.38	18.2	32.54	32.38	(0.48)	17.36	17.76	(2.28)
141	21.28	10.2	17.48	17.41	(0.39)	17.88	18.20	(1.80)
165	33.97	20.4	28.37	27.71	(2.32)	16.49	18.43	(11.77)
172	42.46	23.4	35.99	34.77	(3.38)	15.25	18.11	(18.79)
157	31.02	16.6	24.79	25.38	(2.38)	20.10	18.19	(9.47)
161	38.78	19.2	32.26	31.84	(1.33)	16.80	17.91	(6.58)
150	33.79	14.8	27.80	27.8	(0.01)	17.73	17.72	(0.05)
158	38.00	17.4	31.69	31.25	(1.36)	16.62	17.75	(6.83)
167	31.96	15.2	26.80	26.23	(2.11)	16.15	17.92	(10.94)
157	23.84	13.4	19.61	19.43	(0.92)	17.72	18.48	(4.29)
148	24.24	11.8	19.94	19.84	(0.51)	17.72	18.14	(2.37)
143	23.68	11.8	19.52	19.37	(0.80)	17.55	18.20	(3.74)
Mean PE's					(1.67)			(7.40)

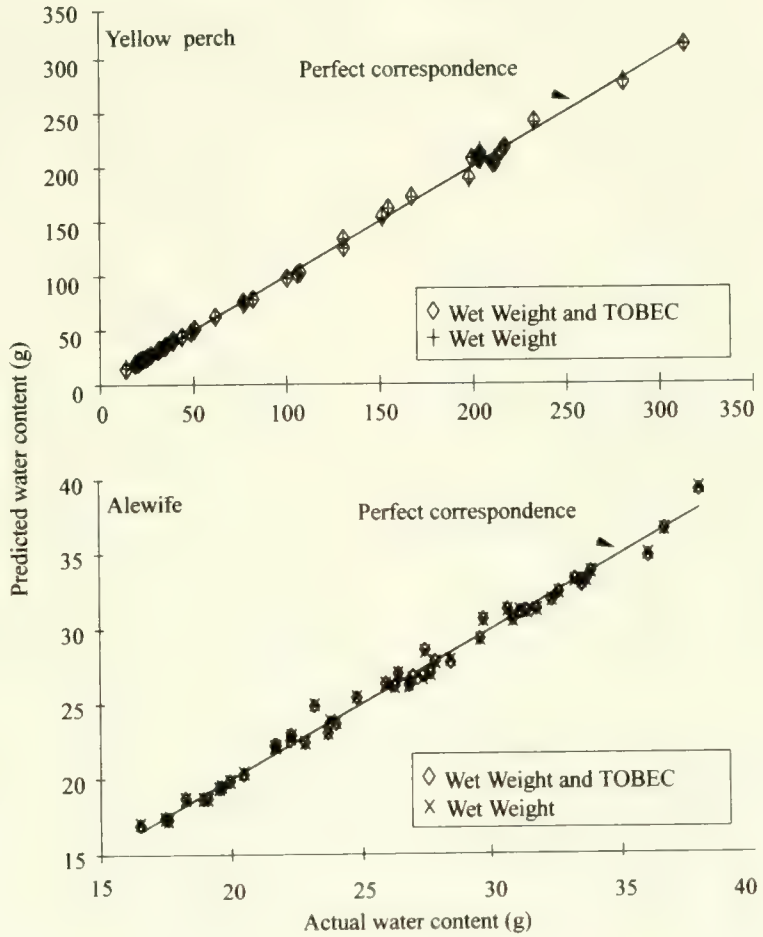

Figure 1

Comparison of the predicted and measured values of water content (g) of yellow perch and alewife. Predicted values are from multiple linear regressions with wet weight and total body electrical conductivity (TOBEC) as independent variables and from simple linear regressions with wet weight as the only independent variable.

The equation for alewife was

$$WC = -0.17206 + 0.8471 \times WWT - 0.0439 \times TOBEC \quad (r^2=0.990).$$

The slope coefficient for wet weight and the intercept in the yellow perch regression model were both significant ($P<0.01$), whereas the *TOBEC* coefficient was not ($P=0.529$). The slope coefficient for wet weight in the alewife regression was significant ($P<0.0001$), whereas both the *TOBEC* coefficient and the intercept were not ($P=0.295$ and 0.679, respectively). Both the yellow perch and alewife predictive equations provided good fit to the data for water content with mean *PE*s from all values in each data set of 3.33% and 1.67%, respectively. Wet weight, however, accounted for most of the variance within each relationship. When wet weight was used as the only independent variable in each regression model, r^2 values were both about 0.99, and were greater than the r^2 values from regressions that used only *TOBEC* as the independent variable. Predictions from these simple linear regressions (*WWT* as the only independent variable) provided nearly as good a fit to the data as the multiple linear regressions (r^2 values decreased only by about 0.00002 to 0.0005, Fig. 1).

Total length and *TOBEC* were not linearly related to water content for yellow perch. Natural log transformations for total length (Ln*TL*) and square root transformations of *TOBEC* values (sq*TOBEC*) re-

turned linear trends. When we replaced *TOBEC* with sq*TOBEC* in the regression model for yellow perch to account for nonlinearity, the r^2 value increased slightly (+0.0002) and the mean percentage error decreased (Table 1). The new yellow perch equation became

$$WC = 0.767 + 0.638 \times WWT + 0.996 \times \text{sq}TOBEC \quad (r^2=0.998).$$

Backwards stepwise multiple linear regression analysis of the yellow perch data eliminated Ln*TL* from the regression model and indicated that four other independent variables (*WWT*, sq*TOBEC*, *TL*, and an offset constant) be included. The inclusion of *TL* in the new regression model increased the r^2 value by only 0.0002, but the mean *PE* also increased to 2.56% in the new model from 2.23% in the model that included only *WWT* and sq*TOBEC*. Backwards stepwise multiple linear regression analysis of the alewife data indicated that only *WWT* was a sufficient predictor of water content in that data set.

Percentage errors in predicted values for water content were consistently larger than the mean *PE*s for *TOBEC* values ≤ 15 (<30 g yellow perch; <35 g alewife; Tables 1 and 2). Previous work indicated that the scanner is accurate for predicting lean body mass in birds down to a body weight of 20 g (Castro et. al. 1990). We found that fish sizes that returned *TOBEC* values below 10 yielded such poor results that we did not include them in our analysis (<24 g yellow perch; <16 g alewife).

Discussion

In fish, water content of the individual is strongly correlated with the whole-body wet weight and, hence, many relationships developed for the EM-SCAN use wet weight as an independent variable (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994). Although wet weight alone could be used to predict many of these values, assessment of the subtle differences in tissue constituents relevant to energy-balance calculations could not be accomplished. Many studies on terrestrial vertebrates have used TOBEC alone to predict tissue composition (Presta et al., 1983; Keim et al., 1988; Walsberg, 1988; Castro et al., 1990); however, all fish TOBEC studies to date have used wet weight and TOBEC as the predictor variables in regression functions. In our work, TOBEC values did not increase the predictive ability of regression functions with wet weight as the other independent variable.

Three previous studies have indicated that TOBEC can accurately predict water content in fish (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994). Each study indicated that TOBEC and wet weight values were correlated to body tissue constituents and water content. The inclusion of TOBEC values in regressions with wet weight as the other predictor of whole-body body water content produced slight increases in r^2 values and decreased the mean square error. We ran regression analyses with backwards stepwise elimination and found that TOBEC was eliminated from the sunshine bass data set (Brown et al., 1993) when wet weight was untransformed but was included when wet weight was $\log_e$ transformed. The regressions for sunshine bass with untransformed wet weight alone and combined with TOBEC both produced lower PEs (2.6 and 2.5 respectively) than did the Brown et al. (1993) equation with $\log_e$-transformed wet weight (PE=3.9). TOBEC was significant in regressions with wet weight for red drum (Bai et al., 1994) and channel catfish (Jaramillo et al., 1994). In these data sets, regressions, including the TOBEC variable, increased the PE from 2.2 to 3.0 for red drum (Bai et al., 1994) and decreased the PE from 4.0 to 2.7 for channel catfish (Jaramillo et al., 1994) versus the regressions with wet weight as the only independent variable. Inclusion of TOBEC values in regressions with wet weight did not substantially or consistently improve the predictions of water content over simple linear regressions with wet weight alone.

When fat is burned and replaced by water in a fish, changes in the total quantity of electrolytic salts should be reflected in TOBEC values. Hence, TOBEC values alone should be able to successfully predict water content. TOBEC values alone can predict water content values in terrestial vertebrates (r^2>0.80) and fish (r^2=0.67 to 0.988). In fish however, TOBEC predicted total wet weight equally well. If more than just test animal size affects conductivity readings, then evidence of changes in the total body content of electrolytic salts should also be apparent when TOBEC and water content values are divided by wet weight. Wet-weight–standardized TOBEC and water content values were not related for alewife, sunshine bass, or red drum (Fig. 2). The apparent trend in the yellow perch data is counterintuitive (Fig. 2) to the expected trend of increased conductance with increased water content. The strength of predictive equations for fish in the above four data sets may be solely due to effects from fish size (e.g. serum and cellular fluid volumes). The expected relationship for these parameters is apparent in our plot of the test data set from Jaramillo et al. (1994; Fig. 2). The nutrient content of diets fed to fish in those experiments was carefully controlled within groups and varied only between groups. Evidence from our study indicates some promise for using TOBEC for fish in situ-

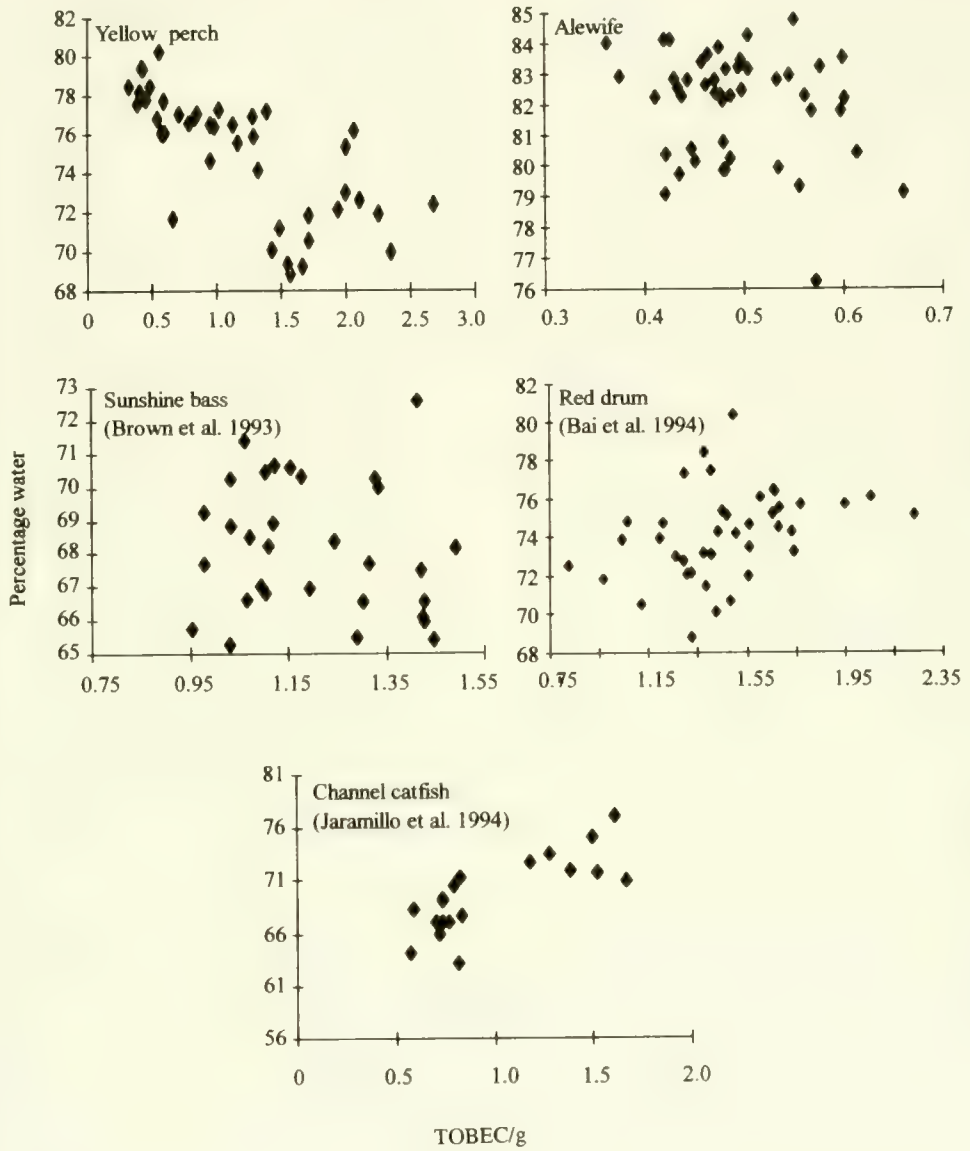

Figure 2

Comparisons between standardized values of percentage water (water content/wet weight) and total-body electrical conductivity (TOBEC/wet weight) for yellow perch, alewife, sunshine bass, red drum, and channel catfish. Data for sunshine bass, red drum, and channel catfish are from Brown et al. (1993), Bai et al. (1994), and Jaramillo et al. (1994).

ations where nutritional status can be controlled (e.g. in aquaculture) and electrolytic balance is given sufficient time to equilibrate throughout all bodily fluid (i.e. serum, cellular, and extracellular) compartments.

Our ultimate goal was to use our predictions of water content to assess the energy content of yellow perch and alewife. Our energy density relationships (Rand et al., 1994; Lantry, 1997) use percentage dry weight as the independent variable. Percentage dry weight values calculated from predicted water content did not, however, correspond to values calculated from measured water content for any of the five fish species used in TOBEC studies (Fig. 3). Our analysis indicates that further evaluations of the use of TOBEC to predict fish body composition are warranted. Fish size should be constrained to narrow ranges, and percentage water {(water content / wet weight) × 100} between individuals of different condition should be evaluated. By controlling fish size, conductivity differences due to body geometry could

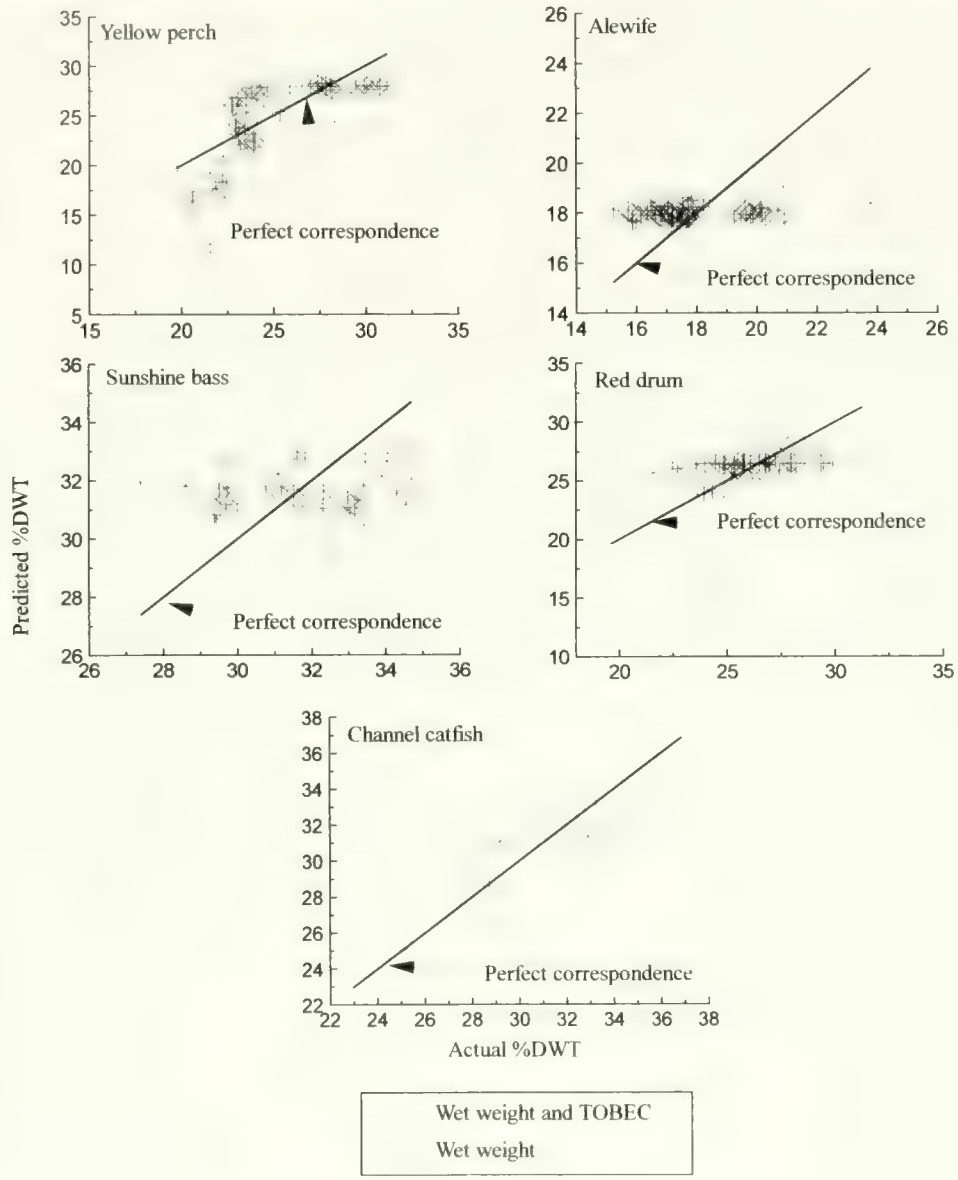

Figure 3

Comparisons between actual and predicted values of percentage dry weight (dry weight/wet weight) for yellow perch, alewife, sunshine bass, red drum, and channel catfish. Data for sunshine bass, red drum, and channel catfish are from Brown et al. (1993), Bai et al. (1994), and Jaramillo et al. (1994). The line in each panel represents the location of equivalence between actual and predicted.

be reduced and wet weight could be eliminated from prediction equations.

Variability associated with the scanning equipment, fish preparation prior to scanning, fish condition, and geometry of fish within the scanner chamber may generate errors too high to accurately predict ecologically significant changes in fish body composition. Analysis of TOBEC readings taken in fish fed, fasted, frozen, and thawed in Bai et al.'s study (1994) indicates that both physiological and physical states affect conductivity values. Dehydration in terrestial animals has also been observed to cause disproportionate changes in TOBEC values (Walsberg, 1988). Our fish were frozen in water and probably were not dehydrated; however, the death of the fish and the effect of freezing and thawing may have altered conductance. Also, the potential existed for exchange between body water and the water sur-

rounding the fish during freezing and thawing. The measurement of TOBEC values, however, did not produce consistent improvement in the predictability of whole-body water content in fish from any of the five data sets considered. This analysis indicates that TOBEC procedures will not be able to predict with sufficient accuracy the water content of fish sampled from field situations and frozen in water for later analysis.

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Abstract.—We measured age and growth of larval striped bass (*Morone saxatilis*) and white perch (*M. americana*) and tested whether growth and survival were enhanced in relation to a seasonal pulse ("bloom") of high zooplankton abundance. Growth rates were lowest before the zooplankton bloom and highest afterwards for both fish species. An index of recruitment potential (instantaneous growth rate, G, divided by instantaneous mortality rate, Z) did not relate clearly to either water temperature or to zooplankton abundance in the case of striped bass but did relate to both factors for white perch. Retrospective analysis of hatch dates in recruited juvenile striped bass from the same year class indicated that later, faster growing cohorts were under-represented when compared to the larval cohort distribution, and that cohorts that co-occurred with high densities of the cladoceran zooplankton *Bosmina freyi* were over-represented. Comparison of these results with similar analyses from other systems suggests that biotic controls on year-class strength may predominate in estuarine systems where physical factors are relatively damped (Hudson) but may play relatively minor roles in those systems with high physical variability.

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Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River

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Survival during the first year of life determines the year-class strength of many fish. The degree to which biotic or physical factors regulate recruitment of fish from larval to juvenile stages varies from one aquatic system to another, and even temporally within systems (Leggett and DeBlois, 1994). The factors promoting or inhibiting recruitment are a subject of intense interest both in theoretical analysis and practical management of fish populations (cf. Hilborn and Walters, 1992). Mortality of young fish below harvestable size is difficult to observe and difficult to measure by means of standard approaches to population assessment (e.g. mark and recapture).

The age and growth rates of young fish, however, can be precisely quantified with otolith analysis (cf. Campana and Neilson, 1985; Secor et al., 1995). This technique has permitted the determination of hatching dates, age, and growth rates of both larvae and juveniles of many species. Comparisons of hatching dates and growth between life stages (e.g. larvae vs. juveniles) allow inferences about the fates of larvae. For example, if larval survival is particularly high during a specific time period, analysis of juvenile hatch dates should reflect the differential survival (assuming adequate sampling). These measures can also be used with repeated samplings of the population to track the growth and mortality of specific age classes (e.g. weekly cohorts) over time. Relationships between these cohort-based rates can be analyzed with respect to variables such as food availability, predation, and the physicochemical environment.

We previously documented that larval striped bass (*Morone saxatilis*) and white perch (*M. americana*), which co-occurred with increases in crustacean zooplankton in the tidal Hudson River, showed a potential energetic advantage compared with larvae that preceded the zooplankton increase (Limburg et al., 1997). A major increase ("bloom") in zooplankton in early summer is a key feature of the Hudson estuary. Larvae occurring before the bloom are exposed to sparse zooplankton densities and low temperature, both of which are associated with mortality risks (Rogers and Westin, 1981; Chesney, 1989; Margulies, 1989; Uphoff, 1989; Tsai, 1991; Cowan et al., 1993). Larvae occurring during and after the bloom have high consump-

tion rates and are at lower risk of exposure to suboptimal or lethal temperatures.

Do these temperature and food conditions translate into differential survival conditions for larval *Morone* spp. in the Hudson River? We addressed this question using methods of otolith age and growth-rate reconstruction. Specifically, we tested if periods of high food availability (zooplankton bloom conditions) were also periods of high larval growth rates. Further, by analyzing the otoliths of juveniles of the same year class (i.e. successful recruits from the larval stage), we also assessed whether or not fish that survived the larval period had high larval growth rates and hatching dates associated with the zooplankton bloom.

Studies of *Morone saxatilis* in Chesapeake Bay tributaries have used both interannual variations in larval abundance (Uphoff, 1989) and cohort analysis methods (Rutherford and Houde, 1995; Secor and Houde, 1995; Rutherford et al., 1997) to establish that rapid drops in water temperature below 12°C virtually eliminate larval cohorts. These studies concluded that the frequency of low temperature events can be an important factor in the recruitment of striped bass in those systems. In contrast, Pace et al. (1993) found no evidence that temperature affected interannual variation of *Morone* spp. recruitment in the Hudson River, although Dey (1981) presented evidence for temperature-induced mortality in Hudson River striped bass in 1976 (temperature dropped suddenly from 15° to 12°C in late May). Thus temperature effects, although not detectable among years, might still manifest themselves as seasonal variability. In this paper we examine the 1994 year classes of striped bass and white perch, including an appraisal of the relation of zooplankton abundance and temperature to growth and mortality of individual cohorts. With this information, we can make tentative comparisons between analyses for the Hudson River and Chesapeake Bay.

Materials and methods

The Hudson River, a partially stratified estuarine-river system in New York State, is tidal up to the Green Island dam, 245 river kilometers (rkm) from the mouth. All life stages of white perch are found throughout the oligohaline and freshwater sections of the estuary (Klauda et al., 1988). Striped bass adults migrate into the estuary in spring to spawn. Larvae are found in both freshwater and oligohaline sections (Boreman and Klauda, 1988). Juveniles spread throughout the estuary and move seaward during late summer and fall (Dovel, 1992).

Larval collections and preparation

Field collections of larval *Morone* spp. were undertaken in the spring and early summer of 1994. Sampling details are described in Limburg et al. (1997). Briefly, three sites, in the upper (Kingston, rkm 148), middle (New Hamburg, rkm 105), and lower (Haverstraw Bay, rkm 65–70) portions of the estuary were sampled between 18 May and 6 July; all sites overlapped with spawning areas. Sampling frequency was designed to examine larval and zooplankton dynamics before, during, and after the intensive bloom of the cladoceran zooplankton *Bosmina freyi* (=*Bosmina longirostris* with older nomenclature). Fish were collected during the daytime with 5-min oblique tows of 0.5-m diameter bongo nets (500-mm mesh). Five replicate tows were conducted at each site on each date. Samples were preserved in 100% ethanol which, when diluted with the sample, reached a final concentration of no less than 75%. Care was taken not to over-dilute the samples below this concentration because of risk of otolith erosion (Brothers, 1987).

In the laboratory, fish were sorted by family and stored in fresh 100% ethanol. Three replicates were chosen at random from the five available at individual stations for each sampling date, and up to twenty *Morone* individuals were arbitrarily selected from each replicate; more replicates were used when larval abundances were low. The larvae were rehydrated, soaked for 15 min in sodium borate buffer solution (30% saturated sodium borate), and then cleared by adding a small quantity of trypsin to the buffer solution. *Morone* larvae were measured to 0.1 mm notochord length (NL) and identified to species by a combination of internal and external characters (Limburg et al., 1997). Lengths were not corrected for preservation shrinkage, but rehydration and clearing fully relaxed constricted musculature so that lengths were readily measured. Otoliths were visible under 25× magnification on a stereomicroscope. Fine insect pins, the tips of which were sharpened further, were used to dissect the sagittal otoliths. Otoliths of fish less than 5 mm NL were cleaned in deionized water and placed directly in mineral oil for later viewing. Following the suggestion of Rutherford (1992), otoliths of larger (>5 mm NL) fish were embedded in Spurr's epoxy, then ground and polished with a series of increasingly fine grinding papers (down to 3 mm).

Juvenile fish collection and preparation

In order to make comparisons between recruited juveniles and larvae, we obtained a total of 218 juve-

nile striped bass from five sites along the Hudson River (at river kilometers (rkm) 40, 63, 95, 114, and 201) during July (n=37), August (n=88), and September (n=93) from state-run fishery surveys. Fish were collected either with a 30.5-m (100-ft) beach seine with 6.1-m bag, 0.64-cm mesh, or with a 61-m (200-ft) beach seine with 1.27-cm stretch mesh (0.64 cm square). Fish were held on ice in the field, then stored frozen.

In the laboratory, juvenile striped bass were defrosted, and standard, fork, and total lengths (SL, FL, and TL respectively) were measured. Sagittal otoliths were removed from each fish, cleaned in 10% sodium hypochlorite (bleach), and embedded in Spurr's epoxy. One otolith from each pair was subsequently sectioned along the transverse axis and prepared in thin section according to the method of Secor et al. (1991). A total of 63 juvenile otoliths were successfully prepared and read.

Otolith microstructure analysis

Otolith microstructure was examined with a light microscope with a video attachment connected to an image analysis system. Specimens were viewed in the sagittal plane by using the digital image for projection. Most specimens were viewed at magnifications of 500–750×, but 1250× (100× objective) was used to resolve the finest increments. Increments were counted several times and averaged. Larval otoliths were examined by one reader, and two independent readers were used to cross-check the consistency of increment counts for juvenile striped bass otoliths.

Ages were estimated by correcting for the effect of temperature on the timing of first increment deposition (Houde and Morin[1]). Age at first increment deposition was estimated as (11.56–0.45 T) for striped bass and (9.05–0.32T) for white perch, where T is water temperature (Houde and Morin[1]). From our measurements of water temperature (n=30) from 14 April to 19 July 1994, we estimated a linear increase in river temperatures over the study period with the regression

$$Water\ temperature = -17.6 + 0.23 \times (day\ of\ year) \quad [r^2=0.98,\ P<10^{-4}].$$

We used this equation to estimate water temperatures on the day of the first increment and assumed little change in temperature back to the hatching day. Ages were estimated as number of increments + temperature adjustment; hatching dates were then backcalculated from the date of capture.

Image analysis was used to measure increment widths. For larvae, widths of the total number of increments on an otolith were measured and averaged to obtain an average daily increment width (in mm). In addition, when possible, widths of the first five increments (I1–I5) and of the sixth and seventh increments (I6–I7) were measured to obtain two standardized estimates of early growth. Increments I1–I5 exhibited slower average growth than did increments I6–I7. In all, otoliths of 248 larval striped bass and 526 larval white perch were examined.

Somatic growth rates were calculated for larvae and juveniles by the equation

$$(L_t - L_{t_0})/Age,$$

where L_t = length at capture; and
L_{t_0} = length at hatch.

L_{t_0} is assumed to be 3.0 mm for white perch and 4.0 mm for striped bass (Mansueti, 1958; Lippson and Moran, 1974). In addition, "standardized" growth rates were calculated for 7-day-old larvae so that comparisons of growth could be made before, during, and after the zooplankton bloom. This was done by determining the number of increments deposited by age 7 (typically <5), multiplying that number by the mean increment width of I1–I5, adding the result to the otolith core radius, and then by using the following regressions to calculate standard lengths at age 7 days:

$$SL_{SB} = -0.37 + 1.95\ (\text{natural log of otolith width}) \quad [r^2= 0.83,\ n=210,\ P<10^{-4}],$$

$$SL_{WP} = -1.67 + 2.18\ (\text{natural log of otolith width}) \quad [r^2= 0.88,\ n=522,\ P<10^{-4}].$$

The same procedure was used to backcalculate age 7-d somatic growth rates for juvenile striped bass.

Mortality and recruitment potential

For purposes of comparison with Chesapeake Bay studies, mortality rates were estimated for fish larvae collected at New Hamburg (rkm 105) by using a method similar to that described in Secor and Houde (1995). Cohort analyses were confined to the New Hamburg station because we were able to collect both species consistently in large numbers. All larvae in these samples were counted, and lengths of at least

[1] Houde, E. D., and L. G. Morin. 1990. Temperature effects on otolith daily increment deposition in striped bass and white perch larvae. International Council for the Exploration of the Sea, Copenhagen, Denmark, Council Meeting 1990/M:5.

100 individuals were measured unless fewer than 100 occurred in the sample. Densities (numbers of fish per 1000 m^3) by 0.5-mm size class were computed and corrected for differences in day and night catch efficiencies, and for extrusion of smallest individuals, by using regressions in Houde et al.[2]

Age distributions of fish collected on different sampling dates were estimated from the otolith-aged fish. Rather than estimate variance from an age–length regression and use it to assign probabilities of age-at-length (Secor and Houde, 1995), we estimated the mean and variance in ages for each 0.5-mm size group and used those parameters to assign age-at-length probabilities (*z*-scores).

The corrected catch densities, separated into 0.5-mm size classes, were multiplied by the appropriate size-based age distributions to obtain numbers of fish of different ages. Following Secor and Houde (1995), hatching dates were calculated and fish were grouped into 6-d cohorts. In some of the cohorts, the age-estimation technique resulted in very small initial numbers of fish. If these numbers were tenfold smaller than the maximum calculated densities of a cohort, they were deleted from the data set. Then mortality rates (Z) of the cohorts were estimated by fitting an exponential decay model to abundances of fish within specific cohorts over time.

We used an index (Rutherford and Houde, 1995; Secor and Houde, 1995) of mean instantaneous growth (estimated for an individual fish as $G = \ln(W_t/W_0)/t$, where t = age at capture, W_t = weight at capture, and W_0 = weight at hatch) over instantaneous mortality rate (G/Z) to compare the benefits accrued in growth versus the costs expressed as mortality for larvae occurring before, during, and after the zooplankton bloom. Weights were estimated from lengths by the equation

$$W = 3.763 \times 10^{-4} \times L^{(4.2879)} \quad [n=67,\ r^2=0.92,\ P<10^{-6}];$$

where W = mg wet weight; and
L = length in mm (Limburg et al., 1997).

Finally, we estimated the dates of first-feeding for striped bass larvae and juveniles with respect to the zooplankton bloom. We assumed that fish begin to feed at day 5 after hatching. We used an age-length regression from the 63 juvenile striped bass to estimate ages of the remaining juveniles. We assumed that little or no out-migration would be occurring in July and August (Dovel, 1992), so that fish collected during these months would show the effect of differential recruitment without the confounding process of out-migration.

Table 1

Mean (± SD) somatic growth rates (GR, mm/d) of larval white perch and striped bass, by site and date, 1994. (n=526 white perch and 248 striped bass; n.d.=no data; — = zero fish in samples.)

	White perch			Striped bass		
Date	Mean GR	SD	n	Mean GR	SD	n
Haverstraw Bay (rkm 65–70)						
18 May	0.181	0.067	15	0.072	0.069	9
24 May	—	—	0	—	—	0
3 June	0.186	0.054	17	0.185	0.111	29
7 June	0.409	0.215	9	0.286	0.128	25
10 June	0.211	0.086	8	0.178	0.111	8
13 June	0.382	—	1	0.250	0.046	17
22 June	0.427	0.199	3	0.293	0.088	36
29 June	0.313	—	1	0.284	0.007	3
6 July	n.d.			n.d.		
New Hamburg (rkm 105)						
18 May	—		0	—		0
24 May	0.155	0.037	37	0.069	0.022	3
3 June	0.192	0.060	47	0.162	0.127	11
7 June	0.218	0.070	42	0.216	0.084	14
10 June	0.236	0.085	35	0.247	0.030	4
13 June	0.210	0.081	29	0.224	0.039	8
22 June	0.265	0.083	11	0.207	0.056	9
29 June	0.306	0.049	11	0.252	0.084	20
6 July	0.331	0.052	9	0.264	0.062	40
Kingston (rkm 148)						
18 May	—		0	—		0
24 May	0.205	0.061	9	0.044	0.027	3
3 June	0.167	0.053	52	0.032	0.054	6
7 June	0.200	0.053	47	0.146	0.189	2
10 June	0.201	0.089	59	0.017	—	1
13 June	0.196	0.086	35	—	—	0
22 June	0.245	0.113	12	—	—	0
29 June	0.300	0.099	37	—	—	0
6 July	n.d.			n.d.		

Results

Growth rates

Mean somatic growth rates (GRs) of both species of *Morone* tended to be lowest prior to the bloom (before 3 June); rates were higher after the bloom (22 June and later), especially for white perch (Table 1;

[2] Houde, E. D., E. J. Chesney, R. M. Nyman, and E. S. Rutherford. 1988. Mortality, growth and growth rate variability of striped bass larvae in Chesapeake subestuaries. Interim Report to Maryland Department of Natural Resources. Chesapeake Biological Laboratory, Solomons, MD. Ref. No. [UMCEES]CBL 88-96, 126 p. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

Fig. 1). There were significant site, species, and site × species effects on mean somatic GRs ($P<10^{-4}$), with highest GRs at the southernmost site (Haverstraw Bay). Mean somatic growth rate for striped bass was 0.053, 0.232, and 0.238 mm/d at Kingston, New Hamburg, and Haverstraw Bay, respectively (greater than an eightfold difference between highest and lowest; it should be noted that the total number of fish sampled at Kingston was very small). Growth rates for white perch did not vary as greatly but did vary in the same longitudinal direction (0.209, 0.215, and 0.245 mm/d at Kingston, New Hamburg, and Haverstraw Bay). Time series of somatic GRs, averaged over all sites for each species (Fig. 1), revealed species-specific patterns of growth with respect to the zooplankton bloom period. Striped bass GRs accelerated more strongly during the bloom period than did GRs of white perch.

Somatic growth rates were related to water temperature as

$$GR = -0.050 + 0.013 \times MWT \quad [r^2=0.15,\ n=774,\ P<10^{-6}],$$

where MWT = mean water temperature during the life of the individual larva (calculated as the temperature midway through the larva's life).

The effect of temperature was removed by calculating residuals of this regression and by using the residuals as a new data set (temperature-adjusted GRs) to assess growth relative to zooplankton dynamics. Temperature-adjusted somatic GRs for white perch showed little trend with respect to the zooplankton bloom, whereas striped bass GRs peaked during the bloom (Fig. 2). This peak was not significantly greater than the adjusted GRs after the bloom, but both differed significantly from the prebloom-adjusted GRs.

Our comparisons of somatic growth rates are based on fish larvae of different sizes and ages. Comparisons of growth rates for a standardized age (we chose age=7 days) can eliminate this potential source of bias. Mean 7-d GRs (Fig. 3) showed a pattern similar to that for overall mean GR, indicating that growth rates did not peak during the zooplankton bloom. Although both species' 7-d GRs varied significantly with respect to the bloom (with highest GRs after the bloom), white perch 7-d GRs did not differ significantly from striped bass 7-d GRs.

Recruitment potential at New Hamburg

Ten 6-d age cohorts, grouped arbitrarily starting 1 May (cohort A) and extending through the period beginning 24 June (cohort J), were identified in the catches at New Hamburg (rkm 105). Insufficient numbers prohibited estimation of Z for the last striped bass cohort (J, 24–29 June) and the last two white perch cohorts (I and J). Estimates of white perch starting densities (natural log of N_0) were highest in early cohorts (A and B; Table 2). Striped bass initial density estimates were highest in later cohorts (E, G, and H; Table 2). Earliest and latest cohorts were poorly estimated owing to low sample numbers.

Estimated mortality rates were highest in cohort A for both species (Table 2). Cohort A (period starting 1 May) appeared only in two samples; presumably recruitment from this group was very low. For white perch, mortality rates declined more or less monotonically with time (and therefore also with increasing temperature). Striped bass mortality rates were also lowest in the latest cohorts, but there did not appear to be a systematic decline (Table 2).

Instantaneous growth rates (G) in striped bass did not vary

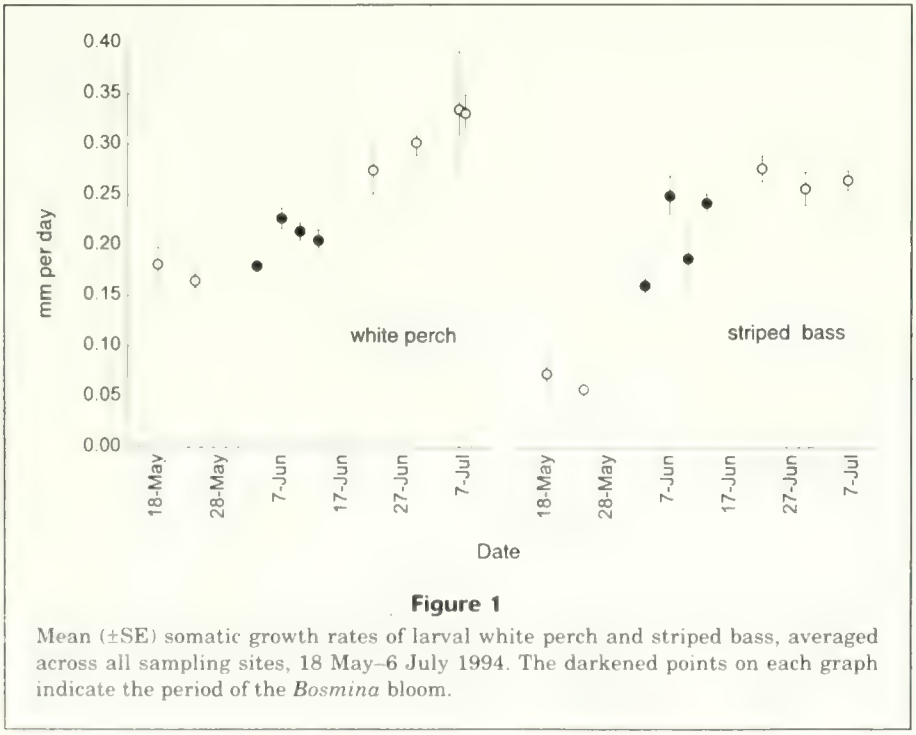

Figure 1

Mean (±SE) somatic growth rates of larval white perch and striped bass, averaged across all sampling sites, 18 May–6 July 1994. The darkened points on each graph indicate the period of the *Bosmina* bloom.

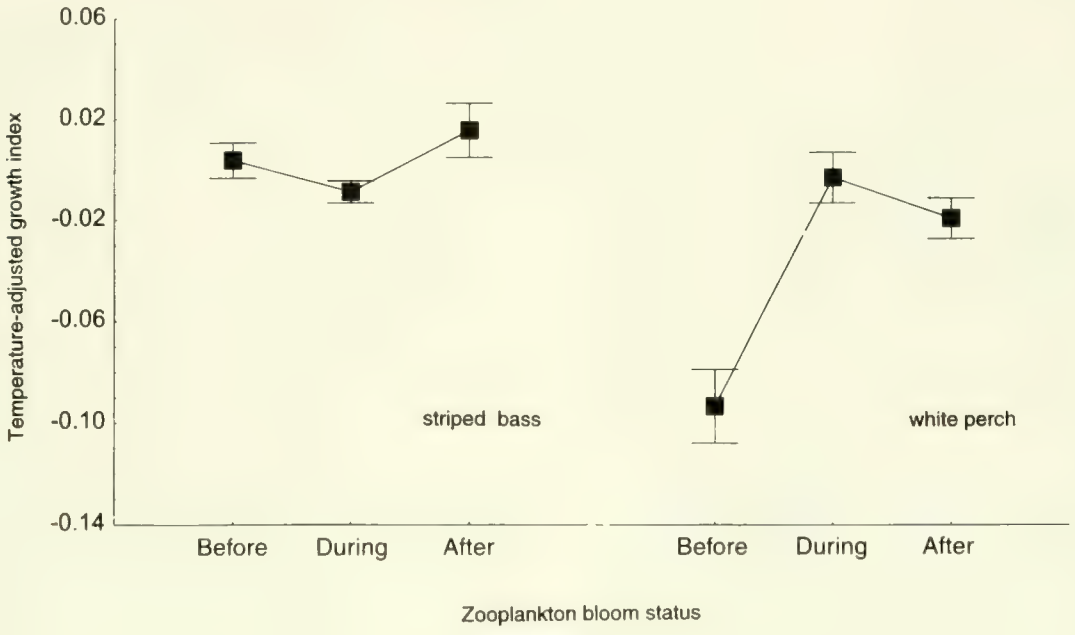

Figure 2

Mean (±SE) somatic growth rates (residuals) of larval white perch and striped bass with the effect of temperature removed, grouped with respect to the *Bosmina* bloom.

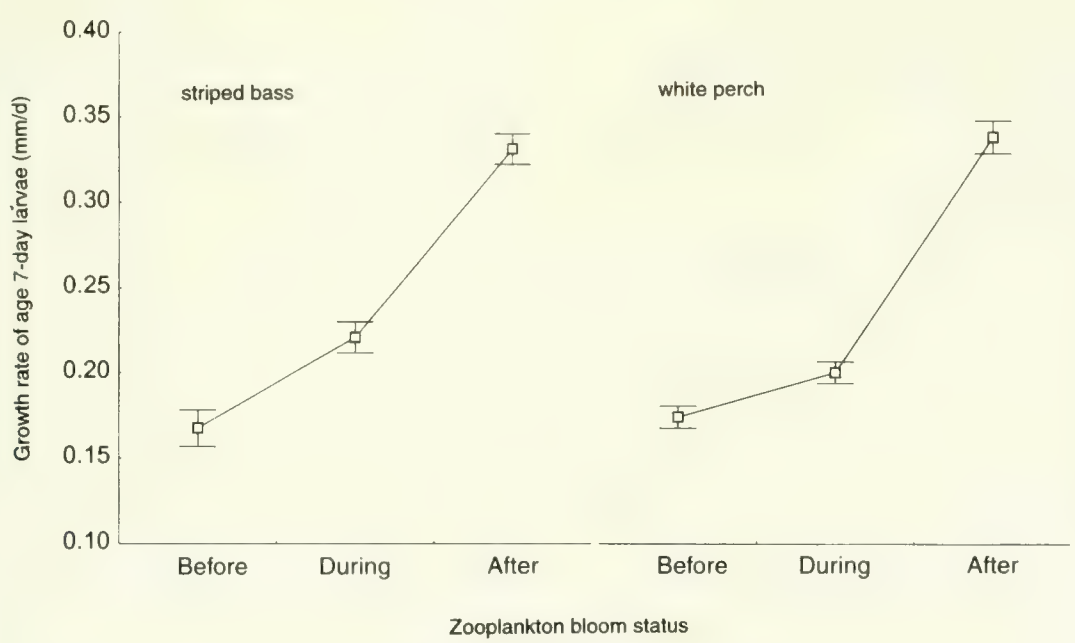

Figure 3

Mean (±SE) growth rates of 7-day old larval white perch and striped bass, grouped with respect to the *Bosmina* bloom.

in a consistent manner, either with temperature or zooplankton density (Table 3). Striped bass G peaked in cohort E (those hatched 25–30 May), as did G/Z. Neither G, Z, nor G/Z for striped bass were significantly affected by either temperature or zooplankton densities estimated during the week of hatching.

Table 2

Estimates of natural logs of initial densities (N_0, numbers per 1000 m^3) and mortality rates (Z) for 6-d cohorts of striped bass and white perch in the Hudson River (New Hamburg site). Letters designate cohorts referred to in text.

Date	Cohort	$\ln(N_0)$	SE	Z	SE	r^2	P	n
Striped bass								
1–6 May	A	4.132		1.51				2
7–12 May	B	7.598	6.153	0.262	0.315	0.41	0.55	3
13–18 May	C	6.919	2.070	0.263	0.132	0.66	0.19	4
18–24 May	D	5.941	2.207	0.296	0.110	0.64	0.05	6
25–30 May	E	7.690	0.751	0.260	0.034	0.94	0.001	6
31 May–5 June	F	6.502	0.549	0.176	0.027	0.91	0.002	6
6–11 June	G	8.808	0.103	0.221	0.005	0.99	0.01	3
12–17 June	H	7.645	0.767	0.163	0.048	0.92	0.18	3
18–23 June	I	6.977		0.145				2
White perch								
1–6 May	A	16.653		0.785				2
7–12 May	B	12.484	2.905	0.509	0.138	0.87	0.07	4
13–18 May	C	9.221	1.299	0.328	0.064	0.87	0.007	6
18–24 May	D	8.058	1.284	0.241	0.064	0.78	0.02	6
25–30 May	E	9.682	1.022	0.304	0.051	0.90	0.004	6
31 May–5 June	F	7.861	0.807	0.187	0.049	0.83	0.03	5
6–11 June	G	5.811	1.295	0.044	0.087	0.21	0.70	3
12–17 June	H	7.885		0.137				2
18–23 June	I	insufficient data						

Table 3

Estimated instantaneous growth (G) rates (± standard error), and index of recruitment potential (G/Z) for 6-d cohorts of larval striped bass (SB) and white perch (WP), New Hamburg (rkm 105), 1994. Calculated water temperatures (see "Methods") and zooplankton densities (copepods and *Bosmina*, no./L), corresponding to each cohort, are included. Zooplankton densities are offset by 5–7 d from actual sample dates (e.g. the zooplankton sample associated with cohort G was collected on 10 June) to approximate the lag in initial feeding by larvae. n.d. = no data. G/Z in parentheses were calculated with the previous cohorts' Z estimates but were not used in analyses.

Cohorts	Dates	Temperature (°C)	Zooplankton density	G_{SB}	SE	G/Z_{SB}	G_{WP}	SE	G/Z_{WP}
A	30 Apr 1994								
B	5 May 1994	12.2	n.d.				0.125	0.006	0.245
C	12 May 1994	13.6	1.88	0.205	0.056	0.779	0.125	0.006	0.380
D	18 May 1994	15.0	10.9	0.205	0.056	0.693	0.141	0.043	0.583
E	24 May 1994	16.4	35	0.564	–	2.169	0.132	0.010	0.436
F	30 May 1994	18.0	80.5	0.070	0.009	0.398	0.159	0.007	0.850
G	05 Jun 1994	19.4	520	0.092	0.012	0.416	0.378	—	8.521
H	11 Jun 1994	20.8	70	0.113	0.021	0.693	0.196	—	1.427
I	17 Jun 1994	22.2	4.1	0.097	0.035	0.671	0.150	0.036	(1.095)
J	23 Jun 1994	23.5	5.6	0.171	0.228	(1.179)			

In contrast, white perch G was significantly correlated with zooplankton density ($G_{WP}=0.136+4.64\times10^{-4}\times(zooplankton\ density)$, $r^2=0.96$, $P<10^{-4}$). The high significance was due to the highest growth at a time of maximum zooplankton density (520 individuals/L), but the regression relationship remained the same even with removal of the influential point. Lowest mean G/Z occurred before the bloom (0.35 ±0.18 SD, $n=4$), intermediate G/Z during the bloom (1.27 ±1.06, $n=2$) and highest afterward (2.53 ±2.04, $n=2$), but these were not significantly different. Although there is a tendency toward increasing G/Z with time (and temperature), it was not statistically significant either.

Table 4

Mean growth (mm/d, calculated from otoliths) at age 7 d after hatching of larval and juvenile striped bass, 1994.

	Bloom status	Mean	SD	*n*
Larvae	Before	0.167	0.072	45
	During	0.221	0.062	47
	After	0.331	0.079	77
Juveniles	Before	0.199	0.080	18
	During	0.215	0.063	33
	After	0.223	0.056	12

Retrospective early life histories of juvenile versus larval striped bass

Larval and juvenile striped bass from the 1994 year class had similar patterns of early growth, as measured by mean growth (mm/d) through age 7 days after hatching. In both groups, growth rates increased monotonically from May through early July corresponding with before, during, and after the zooplankton bloom ($P<0.01$; Table 4). Juvenile mean growth rates before and during the zooplankton bloom were higher (though not significantly so) than larval growth rates in the corresponding periods. However, mean 7-d growth rates of postbloom juveniles were significantly ($F(1,87)=21.03$, $P<10^{-4}$) lower than growth rates of postbloom larvae.

The frequency (distribution of hatching dates) of juvenile striped bass born in the 6-d cohorts beginning 1 May did not correlate well with the index of recruitment (*G/Z*) developed from the larval data (*Frequency*=0.118+0.021 (*G/Z*), $r^2=0.03$).

Because of our ability to "hind-cast" the distribution of hatching dates of juveniles and larvae, we estimated the relative proportions of both larvae and juvenile striped bass that would have begun to feed during the zooplankton bloom (assuming that feeding begins at day 5 after hatching). For this analysis, we analyzed the fish response to *Bosmina* and copepods. For *Bosmina* we assumed that fish with hatching dates between 29 May and 8 June would be able to feed on *Bosmina*; we further assumed that fish hatched between 5 June and 17 June would also be able to take advantage of the bloom of copepods (note that in this analysis we assume that *Bosmina*-feeders occurred above Haverstraw Bay and that copepod feeders occurred throughout the river).

Larval distributions indicated that 37% of the population began to feed after the bloom of *Bosmina* (Fig. 4A), and 26% initiated feeding during the bloom. Of larvae that occurred in the geographic range of *Bosmina* (at New Hamburg and Kingston), over half began to feed after the bloom and less than 20% began feeding during the bloom. In contrast, 44% of juvenile striped

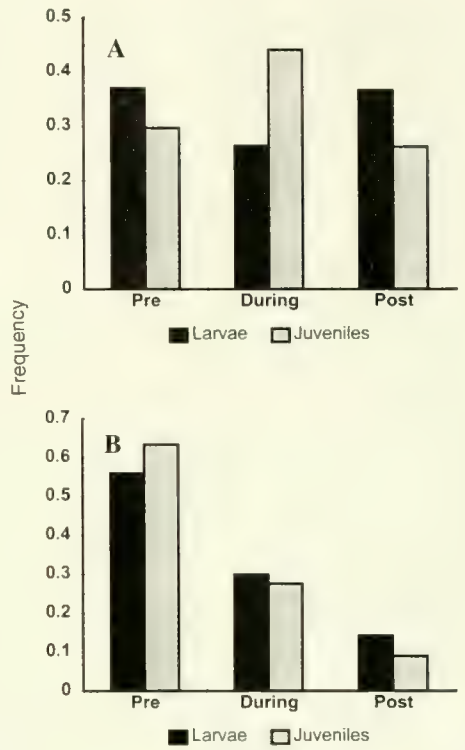

Figure 4

Fraction of larval (black bars) and juvenile (gray bars) 1994 striped bass populations that were estimated to be feeding before, during, and after blooms of (**A**) *Bosmina freyi* and (**B**) copepods in the Hudson River.

bass began to feed during the bloom of *Bosmina* (Fig. 4A); and of the fish identified as first feeding prior to the onset of the bloom, 23% were hatched after 25 May, so that these fish would have been relatively close to first feeding at the time that *Bosmina* numbers increased exponentially. Those survivors to the juvenile stage that began to feed after the *Bosmina* bloom composed the smallest fraction (26%). The first-feeding distributions of larvae and juveniles differed significantly with respect to the *Bosmina* bloom (2×3 contingency analysis, $\chi^2=13.4$, df=2, $P<0.01$), whereas distributions of larvae and juvenile fish with respect to the bloom of copepods did not differ from one another ($\chi^2=3.7$; Fig. 4B). Thus the time period associated with the *Bosmina* bloom, and not the copepod bloom, appears to have been related to successful striped bass recruitment.

Discussion

Evidence from this study provides some support for the relation between larval growth rates and tem-

perature found by Rutherford and Houde (1995) for the Potomac River and Upper Chesapeake Bay and by Secor and Houde (1995) for striped bass larvae in the Patuxent River. However, the relationship we found was weak (r^2 only 0.15). Some measures of growth were also enhanced with increased food availability. Because of the similarity of our approach with that of these previous Chesapeake researchers, we can compare the fates of striped bass larvae in the Chesapeake and Hudson systems.

Temperatures during the larval period were more variable in the Chesapeake tributaries in the studies referred to above than in the Hudson in 1994. In the Patuxent in 1991, water temperatures in April (when nearly 90% of eggs were produced) fluctuated erratically between approximately 13° and 20°C. In May, temperatures rose through the month from 20° to 29°C (Secor and Houde, 1995). In the Potomac (1987–89) and Upper Bay (1988–89) (Rutherford and Houde, 1995), water temperatures also fluctuated, dropping in 1989 during one event from above 16°C to around 12°C, the lower lethal limit for striped bass larvae (Morgan et al., 1981). April and May water temperatures in the Nanticoke, another Chesapeake tributary, also fluctuated in 1992 and 1993 (Kellogg et al.[3]). In contrast, 1994 water temperatures in the Hudson River increased linearly from mid-April through mid-July with little fluctuation.

In spite of the overall warmer temperatures, calculated instantaneous growth rates of larval striped bass grouped into 6-d cohorts were lower in the Patuxent River (mean instantaneous G=0.126/d, range 0.11–0.14) than in the Hudson (mean G=0.190/d, range 0.070–0.564). Nanticoke River growth rates were intermediate (0.166 in 1992, 0.159 in 1993; Kellogg et al.[3]). Hudson striped bass larvae grew at rates similar to those for Potomac River (0.208 and 0.181/d for 1987 and 1989) and Upper Chesapeake Bay larvae (0.183/d). In terms of growth in length, both moronid species in the Hudson grew faster than Patuxent River striped bass larvae (Hudson white perch=0.212 mm/d ±0.101 SD, Hudson striped bass=0.218 mm/d ±0.121 SD, Patuxent striped bass=0.17 mm/d for 0–25 d). Note that Dey (1981) estimated Hudson River striped bass larval growth rates (in 1973–76) as ranging from 0.1 to 0.2 mm/d, based on analysis of weekly changes in mean lengths of larvae. Growth rates in the present study are higher than Dey's estimate and fall within the range of the Potomac (mean growth rates 0.18–0.26 mm/d, 1987–89; Rutherford and Houde, 1995). Differences in growth rates are likely due to a combination of factors in any given year and site; unfortunately, multiyear studies of larval growth rates, which would provide ranges of variation, are few.

An index of population growth, G/Z, has been used as an index of striped bass recruitment success (Rutherford and Houde, 1995, Secor and Houde, 1995, Rutherford et al., 1997, Kellogg et al.[3]) in Chesapeake tributaries because the index corresponded, at least on a seasonal basis, with production of 8-mm larvae, which is, in turn, correlated with year-class strength in the Chesapeake system. The G/Z did not correlate well with our index of recruitment, i.e. juvenile striped bass recruits. We did not examine juvenile recruitment of white perch, nor are we aware of any otolith-based studies of white perch recruitment in other ecosystems.

The G/Z method as applied at New Hamburg must be viewed cautiously, as calculations of mortality (Z) for individual cohorts are based on a few samples and are not well constrained (hence the large standard errors for some cohorts, Table 2). Further, although in aggregate a large number of individuals were examined in this study, growth rates for individual cohorts were estimated from a limited sample size. Finally, there is likely a substantial variability in time and space for both G and Z that currently exceeds measurement capacity even in the most diligent field study. Given these issues of accuracy and precision, our analyses should indicate general trends, but they cannot yet be viewed as conclusive.

In both the Chesapeake Bay and Hudson River, it appears that lowest mortality rates in striped bass larvae fall within a constrained temperature range. Secor and Houde (1995) found a convex parabolic relationship of Patuxent striped bass mortality rates with temperature; minimum mortality rates were associated with cohorts that experienced water temperatures of 16–18°C in the first 25 days of life. Rutherford and Houde (1995) did not find so neat a relationship but rather noted that low mortality rates occurred in early May cohorts of Potomac striped bass larvae, which coincided with water temperatures around 16°C. Mortality rates of Hudson River striped bass in 1994 were also lowest in cohorts associated with water temperatures of 16.4° to 18.0°C during the week of hatching (31 May to 5 June, Table 2); however, first feeding by these cohorts also coincided with the zooplankton blooms. White perch mortality rates appeared to decline with increasing temperature.

[3] Kellogg, L. L., E. D. Houde, and D. H. Secor. 1996. Egg production and environmental factors influencing larval population dynamics in the Nanticoke River, 1992–1993. Chapter 1 *in* E. D. Houde and D. H. Secor (eds.), Episodic water quality events and striped bass recruitment: larval mark-recapture experiments in the Nanticoke River. Final Rep. to Maryland Dep. Natural Resources, Chesapeake Bay Research and Monitoring Division. University of Maryland, Ref. No. [UMCEES]CBL 96-083. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

In the Chesapeake system, temperature can play a key role in setting year-class strength for striped bass (Rutherford and Houde, 1995; Secor and Houde, 1995), although it is not always the determining factor (e.g. Kellogg et al.[3]). Complete failures of individual cohorts were associated with rapid temperature drops down to 12°C (Rutherford and Houde, 1995). Dey (1981) hypothesized that early cohorts of Hudson River striped bass were eliminated by a sudden drop in water temperatures in late May 1976, and simulation analysis by Boreman (1983) supported this inference.

Nevertheless, there was no relationship between temperature and year-class strength for Hudson River moronids over the period 1974–90 (Pace et al., 1993). Examining a 40-yr record of Hudson River temperatures, we found that the likelihood of lethal low temperature events (defined as ≤12°C) declines rapidly during the latter half of April (Fig. 5). Early spawned cohorts of both moronid species have a risk for low-temperature mortality events, but most cohorts are spawned after early May and are highly unlikely to experience this direct source of mortality (Fig. 5).

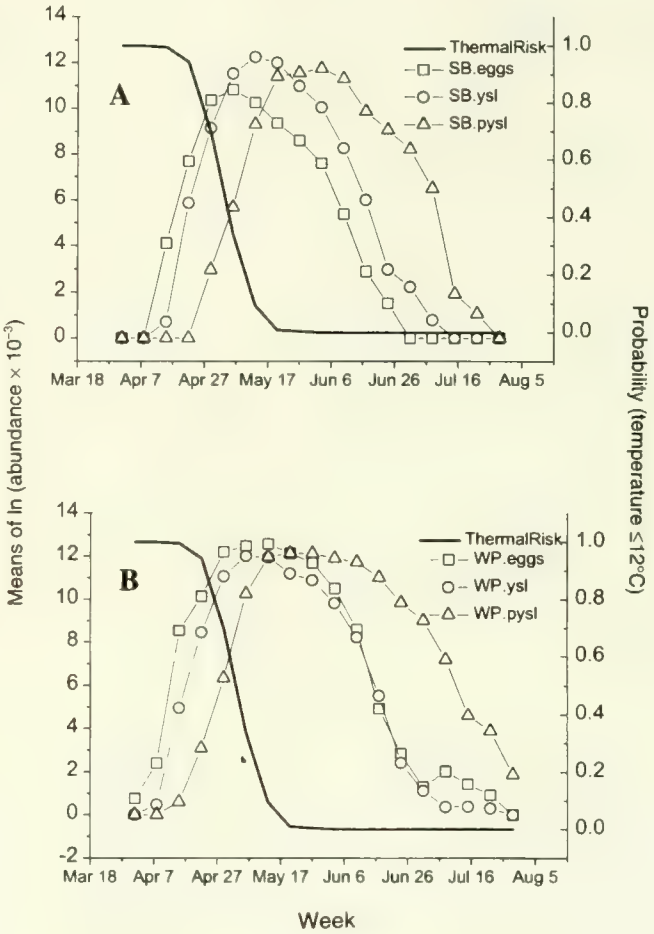

Figure 5

Probability of water temperature occurring at or below 12°C in Hudson River (based on 40-year database: Poughkeepsie Water Works, Poughkeepsie, NY) compared with means of log-transformed, river-wide abundances (1000s) of early life stages of (**A**) striped bass and (**B**) white perch. Squares = eggs, circles = yolksac larvae, and triangles = postyolksac larvae.

We have demonstrated that, like Chesapeake striped bass growth rates, larval moronid growth rates are linked (albeit weakly) to temperature in the Hudson River. Nevertheless, differential mortality occurred on the faster-growing, late cohorts of striped bass. We postulate that this mortality was due to predation. Secor and Houde (1995) also speculated that increased mortality rates observed in late Patuxent cohorts was due to predation. Hudson River moronid larvae that co-occurred with the zooplankton blooms were able to benefit energetically from increased food availability in relation to prebloom conditions (Limburg et al., 1997). Consumption rates continued to be high after the bloom, however, so that energetically the larvae continued to do well. Warmer temperatures after the bloom would have enabled larvae to swim faster and encounter more prey, but they would also potentially have encountered more predators. Thus, we infer that late cohorts suffered differentially greater predation.

We suggest that larger estuarine nurseries, such as the Hudson River, provide more damping of physical fluctuations in characteristics such as water temperature than do smaller estuaries with "flashier" drainage regimes. If this is the case, we might expect Chesapeake Bay moronid stocks to be more at risk for episodic, density-independent mortality events of the type described in Rutherford and Houde (1995). Klauda et al. (1980) noted that striped bass year-class strength, indexed by juvenile abundance, varied about 34-fold in the Hudson River, about 47-fold in Chesapeake Bay, and 160-fold in the Roanoke River (where upstream water temperatures are controlled by water regulation). The different lengths of the data sets, as well as the fact that Chesapeake Bay juvenile index reflects a mix of fish derived from tributaries and the Bay proper, make this comparison somewhat problematic to interpret. What is likely is that increased physical variability in smaller estuaries translate into greater recruitment variability.

Further, evidence from smaller streams suggests that recruitment improves in years with greater spring runoff (McGovern and Olney, 1996; Kellogg

et al.[3]). Increased runoff in small streams could translate into more available habitat for larvae, including greater food availability (Bulak et al. 1997; Kellogg et al.[3]). Larger watercourses like the Hudson should, on average, provide a more constant amount of suitable habitat between years.

Further, we suggest that biotic controls on recruitment, if not as easily assessed as temperature and discharge, may play relatively greater roles in larger estuaries than in smaller ones, or at least in those systems with relatively predictable physical forcing. Our results implicate biotic factors for one year class of striped bass in the Hudson and are based on a comprehensive approach that included careful observation of larvae and retrospective analysis of juvenile early life histories. Had we not carried out the retrospective analysis, we likely would have predicted that later cohorts would have had the greatest recruitment potential.

Acknowledgments

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Abstract—The roudi escolar *Promethichthys prometheus* is common in deep hook-and-line and longline catches of a small-scale fishery along the slope off the Canary Islands. Population structure, reproduction, growth, and mortality of the species were studied from sampling undertaken from August 1992 to July 1995. Range of length of fish in the catches was between 36 and 80 cm TL, with a main distribution between 56 and 66 cm. The overall ratio of males to females was 1:1.74. Females predominated in all sizes. The sex ratio varied throughout the period of study; the lowest discrepancy between males and females, however, was during the reproductive period. A vertical space partitioning among sexes was observed, with males predominating from 600 to 800 m depth, females from 300 to 500 m. The reproductive period of the species was from April to September, with a peak in spawning in June–July. The size at first maturity was 47.41 cm. The parameters of the length-weight relationship for all fish were a=0.004521 and b=2.98932. Age readings of otoliths indicated that the exploited population consisted of nine age groups (III–XI years). The von Bertalanffy growth parameters for all individuals were L_∞=93.61 cm, k=0.18/years, and t_0 =−1.54 years. The rates of mortality for all fish were Z=0.49/years, M=0.35/years, and F=0.14/years. The length at first capture for the whole population was 51.57 cm.

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Biology of a deep benthopelagic fish, roudi escolar *Promethichthys prometheus* (Gempylidae), off the Canary Islands

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The family Gempylidae consists of 16 genera and 23 species. Only seven species are found off the Canary Islands, one of which is the roudi escolar *Promethichthys prometheus* (Cuvier, 1832), the only species recognized to date in the genus *Promethichthys* (Nakamura and Parin, 1993).

The roudi escolar is a benthopelagic marine fish that has a worldwide distribution in tropical and warm temperate waters. This species generally inhabits waters between 100 and 800 m in depth over seamounts and continental and insular slopes. It migrates upward at night, probably forming schools (Nakamura, 1981; Parin, 1986; Nakamura and Parin, 1993).

Published information on *P. prometheus* is very scarce. The majority of studies describe its morphological characteristics, geographical and depth distribution, and ecology (Nakamura, 1981; Parin, 1986; Nishikawa, 1987; Nakamura and Parin, 1993). Only Lorenzo and Pajuelo (1995) have studied some biological aspects of the species. These authors carried out a preliminary study on the sex ratio, reproduction, and age and growth of roudi escolar off the Canary Islands (central-east Atlantic) on the basis of a small number of specimens during one life cycle. This paper is an extension of their work, analyzing, in addition to all those aspects, population structure and mortality.

The roudi escolar is common in the catches of the deep hook-and-line and longline small-scale fishery over the slope off the Canary Islands. In this area, this species is captured year round without significant seasonal differences in landings.

Materials and methods

Between August 1992 and July 1995, the TL (cm) of 1879 specimens of roudi escolar was measured monthly from commercial catches of the small-scale fleet. Fish were caught with baited hook-and-lines and longlines at depths of 285–870 m around the islands of the Canary archipelago (Fig. 1).

A subsample was taken by a random stratified method from each sample for biological examination. In total, 776 individuals were analyzed. For each fish, the TW (0.1 g) and the weight of the gonads (0.01 g) were measured, and sex and stage of maturation were ascertained macroscopically. The latter was classified as follows: I = immature; II = resting; III = ripe; IV = ripe and running; V = spent. Sagittal otoliths of the fish were extracted, cleaned, and stored dry. The length-frequency distribution of individuals in catches was calculated. Data were pooled for 1992–95.

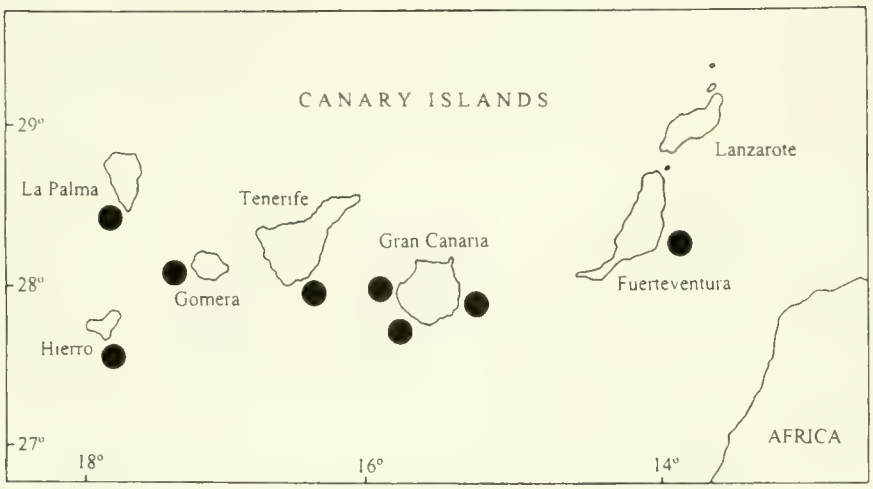

Figure 1
Location of sampling areas (●) in the Canary Islands.

The sex ratios (males:females) for the whole sample, for different size classes, for quarters of a year, and for depth strata were calculated. The reproductive season was determined on the basis of monthly variations of the gonadosomatic index (GSI) according to Anderson and Gutreuter (1983). The length at sexual maturity (length at which fifty percent of the specimens became mature) was estimated by means of a logistic function that was fitted to the proportion of the mature individuals (stages III, IV, and V) by using a nonlinear regression (Saila et al., 1988).

The ratio of total length to total weight was calculated over the whole period for males and females separately, as well as for the population as a whole, by applying a linear regression (Ricker, 1973). Age was determined by interpreting growth rings on the otoliths; whole otoliths were placed in a watch glass with a blackened bottom and containing glycerin and examined under a compound microscope with reflected light. Counts for each specimen were performed at least twice and only coincident readings were accepted. An index of average percent error (APE) developed by Beamish and Fournier (1981) was used to compare the precision of age determinations. Ageing was validated indirectly by examination of monthly changes in appearance of the margins of the otoliths (Morales-Nin, 1987). The date 1 July was considered as birthdate to assign the individual ages to age groups. The von Bertalanffy growth curve was fitted to data of the resulting age-length key by means of the Marquardt's algorithm for nonlinear least squares parameter estimation (Saila et al., 1988).

Length-frequency data were converted to age frequencies by using the estimated von Bertalanffy growth parameters (Pauly, 1983, 1984). The rate of total mortality (Z) was calculated from the length converted catch curve by using ELEFAN program (Gayanilo et al., 1988). The rate of natural mortality (M) was determined from the equation of Pauly (1980). Following estimation of Z and M, the rate of fishing mortality (F) was calculated by substraction. The length at first capture was estimated from the selection ogive generated from the length converted catch curve (Pauly, 1984).

Results

The size-frequency distribution showed a length range of 36 to 80 cm TL in the catches, with a main distribution between 56 and 66 cm (Fig. 2).

Of the 776 fish examined, 282 (36.3%) were male, 491 (63.3%) female. The sex of the remaining 3 (0.4%) individuals could not be identified macroscopically because they were immature and had very thin, translucent gonads. The overall ratio of males to females was 1:1.74 and χ^2 analysis revealed this to be significantly different from a 1:1 ratio (Table 1). Females predominated in all size intervals. Sex ratios for males and females grouped into 5-cm length classes had significant departures from the 1:1 ratio for all size intervals (Table 1). The ratio of males to females varied throughout the period of study, but there were no significant differences from the 1:1 ratio during the spring and summer months (Table 2). There was a relationship between the sex of roudi escolar and depth; males predominated at 600 to 800 m depths, females at 300 to 500 m (Table 3).

The GSI showed higher values for females than for males (Fig. 3). The same temporal variation pat-

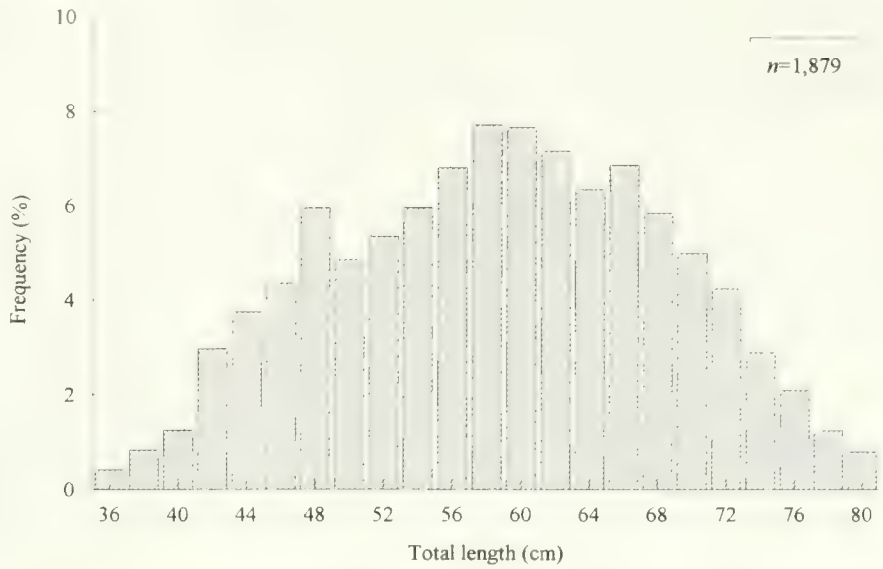

Figure 2

Length-frequency distribution for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

Table 1

Number of males and females of *P. prometheus* caught off the Canary Islands by 5-cm size class and sex ratio tested by chi-square analysis. $^{*}=\chi^2>\chi_t^2{}_{1,0.05}=3.84$.

Length (cm)	Males	Females	Sex ratio	χ^2
35.1–40.0	5	14	1:2.80	4.26*
40.1–45.0	21	40	1:1.90	5.91*
45.1–50.0	29	52	1:1.79	6.53*
50.1–55.0	45	71	1:1.57	5.82*
55.1–60.0	60	94	1.1.56	7.50*
60.1–65.0	48	84	1:1.75	9.80*
65.1–70.0	36	62	1:1.72	6.89*
70.1–75.0	26	48	1:1.76	6.54*
75.1–80.0	12	26	1:2.16	5.15*
Total	282	491	1:1.74	56.50*

Table 2

Number of males and females of *P. prometheus* caught off the Canary Islands by quarter and sex ratio tested by chi-square analysis. $*=\chi^2>\chi_t^2{}_{1,0.05}=3.84$.

Quarter	Males	Females	Sex ratio	χ^2
3/92	16	23	1:1.44	1.25
4/92	13	35	1:2.69	10.08*
1/93	13	37	1:2.85	11.52*
2/93	24	37	1:1.54	2.77
3/93	24	34	1:1.42	1.72
4/93	14	38	1:2.71	11.07*
1/94	29	51	1:1.75	6.05*
2/94	36	49	1:1.36	1.98
3/94	39	50	1:1.28	1.35
4/94	24	44	1:1.83	5.88*
1/95	31	59	1:1.90	8.71*
2/95	19	34	1:1.79	4.24*

tern was recorded for both sexes. Highest values occurred between April and September, peaking during June–July. From October to March the values were low.

No significant difference in length at sexual maturity was found between males and females (t-test, $t=1.31<t_{0.05,385}=1.65$). The length at which fifty percent of the fish became mature was 47.41 cm TL (Fig. 4).

Males were found to be between 38 and 80 cm TL, females between 36 and 80 cm. The length range of immature individuals was from 36 to 38 cm. The parameters of the total length to total weight relationship for males and females separately, and for the population as a whole, are given in Table 4. No significant difference in the allometric coefficient was found between males and females (t-test, $t=1.53<t_{0.05,771}=1.65$). Isometric growth was observed in both sexes and for the whole population (Table 4).

Of the otoliths examined, 670 (86.4%) were readable and used for the study of age and growth. The

APE value was only 3.4%. A false hyaline ring interrupting the normal growth pattern of the otolith was identified within the fourth annual opaque zone and in all subsequent opaque zones. Marginal zone analysis showed that one annulus was formed per year (Fig. 5). The percentage of otoliths with opaque edge was high in the months from April to September, and between June and August in particular.

Fish aged 3 to 11 years were present in the samples (Table 5). Growth parameters determined for males, females, and the entire population are shown in Table 6. No significant differences in the growth parameters were found between sexes (Hotelling's T^2-test, $T^2=5.29<T_{0\ 0.05,3,666}^2=7.88$).

The length converted catch curve is shown in Figure 6. The rates of total mortality, natural mortality, and fishing mortality were $Z=0.49$/year, $M=0.35$/year, and $F=0.14$/ year, respectively. The size at first capture was 51.57 cm TL.

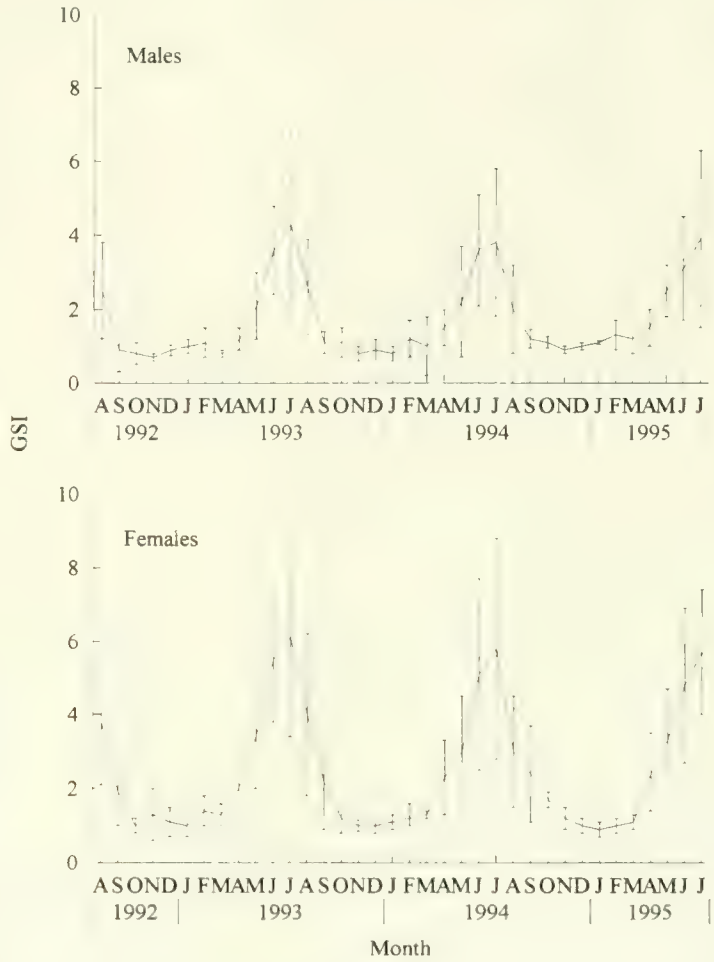

Figure 3

Monthly evolution of the gonadosomatic index (GSI) for males and females of *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

Discussion

Promethichthys prometheus is distributed along the slope to a depth of 800 m (Nakamura and Parin, 1993). In waters off the Canary Islands, greatest concentrations of this species are found between 400 and 700 m depth. Below this depth, the species is replaced by other trichiuroid fish present in the area, e.g. the black scabbardfish, *Aphanopus carbo* Lowe, 1839 (Uiblein et al., 1996).

The roudi escolar off the Canary archipelago is a gonochoristic species with no evidence of sexual dimorphism. The sex ratio is clearly unbalanced in favor of females. This fact could be explained by the differences between sexes in the spatial distribution. The lowest discrepancy between sexes observed during the reproductive season seems to confirm this conclusion. Because of the space partitioning between sexes and because females are fished more than males, this species could be classed as vulnerable to unrestrained fishing. Therefore, fishing for roudi escolar is an activity that has the potential to threaten its target population compared with fishing for more reliable and robust stocks (Csirke, 1988). This fishery will require a prudent exploitation strategy to reduce the potential risk of a collapse.

The roudi escolar has a definite reproductive period (extending from April to September, with a peak in spawning activity in June–July) which agrees with information reported by Parin (1986) and Nakamura and Parin (1993). These authors pointed out that the

Table 3

Number of males and females of *P. prometheus* caught off the Canary Islands by depth stratum and sex ratio tested by chi-square analysis. $^{*}=\chi^2>\chi_{t\ 1\ 0\ 05}^2=3.84$.

Depth (m)	Males	Females	Sex ratio	χ^2
201–300	4	26	1:6.50	16.13*
301–400	21	136	1:6.47	84.23*
401–500	35	187	1:5.34	104.07*
501–600	28	39	1:1.39	1.81
601–700	76	48	1.0.63	6.32*
701–800	85	41	1:0.48	17.12*
801–900	32	12	1.0.37	9.09*

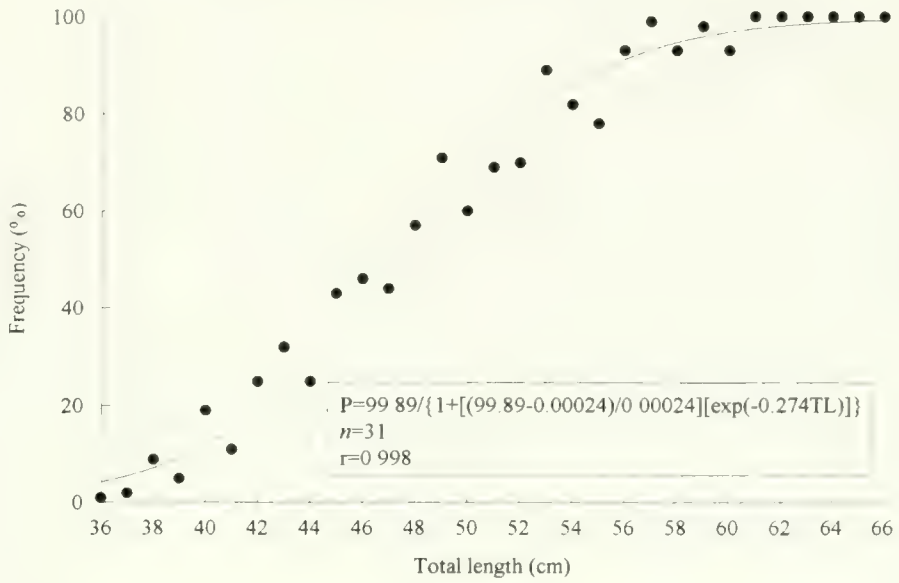

Figure 4

Sexual maturity ogive for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

spawning of this species occurs from August to September in the Atlantic off Madeira. Nishikawa (1987) found the highest concentration of gempylid larvae at the end of the summer months in the Pacific waters of Japan. In the Canary archipelago, the spawning of roudi escolar seems to be related to water temperatures, occurring when these reach greatest values. Possible significance of seasonal temperature variation to maturation and spawning in other bony fish species off the Canary Islands has been discussed by Lorenzo and Pajuelo (1996) and Pajuelo and Lorenzo (1995, 1996). Reproduction in roudi escolar does not involve horizontal migrations because during the spawning season the specimens are observed in the same areas where they are fished all year round. The lowest discrepancy in the number of males and females observed during the spawning period suggests an aggregation for breeding. Males and females were found aggregated mainly at depths of 450–650 m during this period.

Length at sexual maturity does not differ between males and females, corresponds approximately to 48 cm TL. In the age-length relationship, this size corresponds to 4-year-old specimens. The size at which fifty percent of the fish become mature is less than the length at first capture and the majority of the total catch is longer than this length, indicating a good exploitation pattern from the biological point of view. Furthermore, a low value of fishing mortality rate was obtained.

Table 4

Parameters of the length-weight relationship for males, females and all fish of *P. prometheus* caught off the Canary Islands and the possibility of isometry tested by Student's *t*-test. * = $t>t_{0.05,n>250}=1.65$.

	a	*b*	SE(b)	r^2	*n*	*t*-test
Males	0.004128	2.95321	0.03721	0.959	282	1.25
Females	0.004987	2.96214	0.03140	0.981	491	1.20
All fish	0.004521	2.98932	0.02341	0.992	776	0.45

The alternate pattern of opaque with translucent zones was easily distinguishable on the otoliths of the roudi escolar. These zones are deposited owing to alternating periods of rapid and slow growth (Williams and Bedford, 1974). The opaque zone is formed when the water temperature is higher, and food is abundant, and the translucent is formed when temperature is lower and the species spawns. This finding demonstrated the validity of using otoliths for estimating the age and growth of roudi escolar. The false hyaline zones observed within the fourth opaque ring and in subsequent opaque rings are probably spawning bands, because this species spawns in the summer months, when the opaque zone is formed in the otoliths. Morales-Nin (1987) pointed out that when the spawning does not take place during the period of hyaline zone formation, a false ring, known

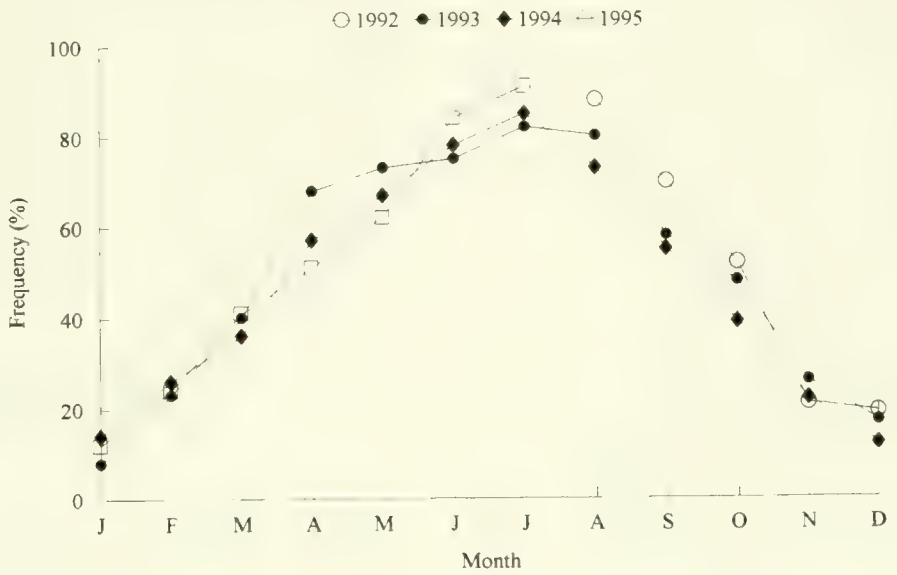

Figure 5

Monthly percentage of otoliths with opaque edge for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

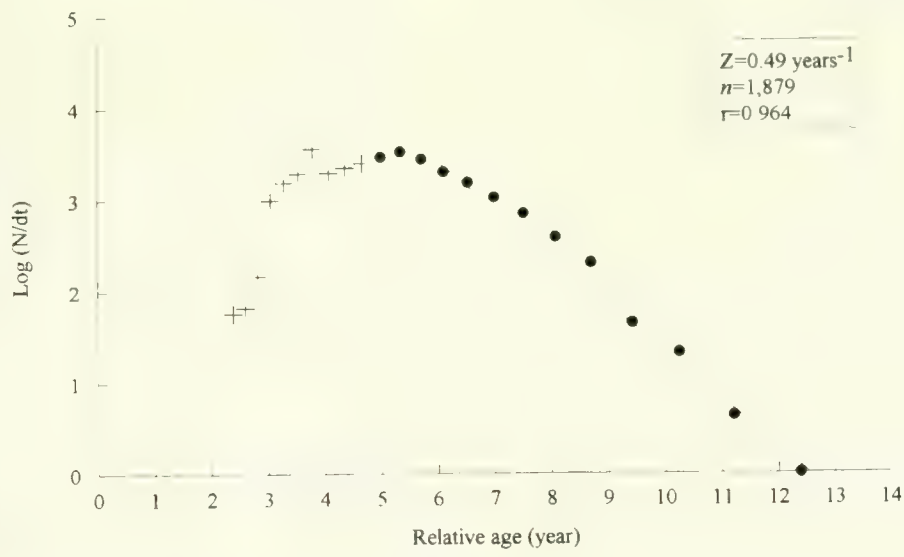

Figure 6

Length converted catch curve for *P. prometheus* caught off the Canary Islands (August 1992–July 1995). The initial data points (+) were not used in the regression.

as a spawning ring, may form within an opaque zone, dividing it into two.

The oldest age class observed was XI years, although this class, as well as age classes IX and X, were poorly represented in the landings. As a whole, growth of the roudi escolar is relatively fast and males and females grow at equal rates. The growth parameters obtained are reasonable because the theoretical maximal length value is greater than the size of the largest fish sampled and because the growth coefficient value indicates relatively rapid attainment of maximal size.

Table 5

Age-length key for all fish of *P. prometheus* caught off the Canary Islands.

Size (cm)	Age group (years) III	IV	V	VI	VII	VIII	IX	X	XI
36	2								
37	1								
38	2								
39	4								
40	6								
41	9								
42	9	1							
43	7	3							
44	4	4							
45	3	8							
46	3	7							
47		9							
48	2	13	1						
49		17	2						
50		14							
51		7	4						
52		5	6						
53		4	8						
54		3	10	1					
55			16	3					
56		2	22	3					
57		1	19	6					
58			12	7					
59			8	11	2				
60			4	17	2				
61			2	28	3				
62			3	21	6				
63			1	11	8				
64				8	14	2			
65				7	20	1			
66				3	23	4			
67				1	16	7			
68				2	10	10	1		
69					6	12	4		
70					3	17	4		
71					2	11	7	1	
72					1	6	9	2	
73						5	9	2	
74						1	7	3	1
75						2	5	6	1
76							2	4	2
77							1	3	2
78									1
79								1	
80									1
n	52	98	118	129	116	78	49	22	8
$\bar{x}$	41.6	48.9	55.7	61.1	65.5	69.4	72.4	74.9	76.7
SD	2.4	2.8	2.6	2.6	2.4	2.2	2.0	1.8	1.7

Table 6

Parameters of the von Bertalanffy growth curve for males, females, and all fish of *P. prometheus* caught off the Canary Islands.

	L_∞ (cm)	k (per year)	t_0 (years)	r^2
Males	91.93	0.18	−1.66	0.964
Females	94.03	0.17	−1.58	0.978
All fish	93.61	0.18	−1.54	0.988

Acknowledgments

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Abstract.—We collected data on age-length and length-weight relationships, age and length at first maturity, and spawning seasons of grass rockfish, *Sebastes rastrelliger*, and brown rockfish, *S. auriculatus*, off southern California. In addition, we also collected data on fecundity of grass rockfish. For both species, males and females grew at the same rates and von Bertalanffy age-length parameters for grass rockfish were l_∞ = 51.3 cm, k = 0.11, t_0 = −2.41 and for brown rockfish l_∞ = 51.4 cm, k = 0.16, t_0 = −0.55. Male and female grass rockfish matured at about the same length and age, between 22 and 28 cm and between 2 and 5 yr. There was also little difference between the sexes for brown rockfish; they matured between 19 and 32 cm and between 3 and 6 yr. Grass rockfish spawned from January to March, peaking during January; brown rockfish spawned from January to June (and perhaps August), also peaking in January. Fecundity of grass rockfish ranged from about 80,000–760,000 eggs.

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Fish. Bull. 87:100–109 (1998).

Aspects of the life histories of grass rockfish, *Sebastes rastrelliger*, and brown rockfish, *S. auriculatus*, from southern California

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Rockfishes (Scorpaenidae: *Sebastes*) are of major commercial importance in California waters. Until recently, almost all of these fishes were landed dead, destined either to be sold whole or as fillets, as fresh or frozen products (Lea, 1992). The sale of live rockfish formed only a very small part of the commercial fishery, and most of this catch was sold in Asian markets and restaurants, particularly in San Francisco and Los Angeles. Recently, however, landings in the live fish fishery have increased sharply. Documented landings (almost certainly an underestimate of the true catch) escalated from about 52,000 pounds in 1989 to 987,000 pounds in 1995 (McKee-Lewis[1]). Live finfish caught in California waters are now widely sold in many local and overseas venues. Within the state, most of the fish destined for the live fish market are caught off southern and central California.

The live-fish fishery targets primarily those inshore species easily held alive, i.e. various rockfishes, California sheephead (*Semicossyphus pulcher*), California halibut (*Paralichthys californicus*) and cabezon (*Scorpaenichthys marmoratus*). Among the important rockfishes are grass rockfish (*S. rastrelliger*) and brown rockfish (*S. auriculatus*). Over 100,000 pounds of grass rockfish were landed in the live fish fishery in 1995 (McKee-Lewis[1]). Despite their importance to this fishery, relatively little was known of their biology.

Before our study, virtually nothing had been published on the life history of grass rockfish. They are solitary crevice-dwellers, inhabiting high relief substratum from Yaquina Bay, Oregon, to Bahia Playa Maria, central Baja California (Miller and Lea, 1972). Grass rockfish are among the shallowest-dwelling rockfishes, found from the intertidal waters to 46 m, usually to depths of about 10 m (Feder et al., 1974; Eschmeyer et al., 1983; Yoshiyama et al., 1986). Grass rockfish feed on fishes, crabs, shrimps, and other crustaceans (Quast, 1968; Grossman, 1986).

Somewhat more was known regarding brown rockfish, which range from Prince William Sound, northern Gulf of Alaska, to Bahia San Hipolito, central Baja California, and which inhabit subtidal waters to depths of 135 m (Love et al.[2]). Unlike grass rockfish, brown

[1] McKee-Lewis, K. 1994. California Department of Fish and Game, Marine Resources Division, 4949 Viewridge Ave., San Diego, CA. Personal commun.

[2] Love, M. S., L. Thorsteinson, C. W. Mecklenburg and T. A. Mecklenburg. 1998. A checklist of marine and estuarine fishes of the Northeast Pacific, from Alaska to Baja California. Biological Resources Division, U. S. Geological Survey.

rockfish may be found in small aggregations. The young are often found in nearshore bays, often around piers or over rubble. Older fish tend to move out of shallow waters and live over both high and low relief, often near the sand-rock interface (Matthews, 1990; Adams, 1992). Brown rockfish feed on crustaceans and fishes (Quast, 1968; Washington et al.[3]). In Puget Sound, spawning occurs during June, whereas off central California larvae are released in December–January and May–June (Wyllie Echeverria, 1987; Washington et al.[3]). There has been no published information on growth rates. In addition, despite their importance, little work on this species has been conducted in southern California.

Knowledge of the life history of a species is an essential prerequisite for effective fisheries management. Our goal was to fill gaps in knowledge of the basic life history of these two species in southern California waters.

Methods

We collected 162 grass rockfish during 1984 and 1996 and 367 brown rockfish between 1977 and 1995. All were collected from southern California waters by spear or hook and line. Data collected included total length (cm), weight (g), sex, capture location, and collection date. In the laboratory, we weighed the gonads, assessed reproductive state, and removed sagittal otoliths.

Age determination

Otoliths were placed on wood blocks and embedded in clear epoxy. Each block with its otoliths was placed on a Buehler Isomet low-speed saw, and an 0.05-cm wafer (transverse section) was cut from it with two diamond-edge blades separated by a stainless steel shim. Before reading, the wafers were burned slightly over an alcohol lamp. The wafers were then placed in a water-filled, black-bottomed watch glass and examined under a dissecting microscope.

Ages were assigned by direct observation of otolith annuli. We aged a total of 149 grass rockfish, including 78 males (16.6–47.5 cm) and 71 females (14.4–50.5 cm), as well as 269 brown rockfish, including 120 males ranging in length from 15.0 to 49.8 cm and 149 females ranging from 17.2 to 53.2 cm. Growth was assumed to be described by the von Bertalanffy growth curve model (von Bertalanffy, 1938):

$$l_t = l_\infty \left(1 - e^{-k(t-t_0)}\right),$$

where l_t = length at time t;
l_∞ = theoretical maximum length;
k = constant expressing the rate of approach to l_∞; and
t_0 = theoretical age at which $l_t = 0$.

Growth equation constants for the von Bertalanffy growth model were calculated from length-at-age data for each species by using the least-squares, nonlinear regression (SYSTAT, 1992).

Maturation and reproduction

We estimated length and age at first maturity by classifying gonads as immature or mature on the basis of criteria given in Westrheim (1975), Gunderson (1977), and Love and Westphal (1981). As with other rockfishes, it was difficult to distinguish between immature and mature resting-stage females during the nonreproductive season. Thus, we did not use females captured during the nonreproductive season for either the length-maturity or age-maturity analyses.

The relationships between length and maturity and age and maturity were established by using a natural log transformation of the equation

$$P_x = \frac{1}{1 + e^{ax+b}}$$

(Gunderson et al., 1980) to yield

$$\ln \frac{(1 - P_x)}{P_x} = ax + b,$$

where p_x = the proportion mature at length or age x; and
a and b = fitted parameters.

We then plotted x against

$$\ln \frac{1 - P_x}{P_x}$$

using simple linear regression to estimate values for a and b. Fifty-percent maturity was calculated by using fitted values of a and b, and by using $p_x = 0.50$ to solve for x.

A gonadosomatic index [(gonad weight)/(total body weight) × 100] was computed to quantify changes in gonad size with season. Gonad condition (immature, resting, vitellogenesis, eyed, spawned [Wyllie Echeverria, 1987]) was determined for each female.

We determined egg production in grass rockfish, counting subsamples of unfertilized eggs. Eggs were

[3] Washington, P. M., R. Gowan, and D. H. Ito. 1978. A biological report on eight species of rockfish *Sebastes* spp. from Puget Sound, Washington. Northeast Alaska Fisheries Center, Processed Rep., 50 p.

excised from the ovarian membrane and placed in Gilson's solution (equal parts concentrated glacial acetic acid, chloroform, and 60% ethanol) for about three months and shaken periodically to loosen them from ovarian tissue. Before counting, the ovaries were repeatedly washed and the egg masses broken up to remove remaining connective tissue. The resulting eggs were weighed; the subsamples were removed and also weighed. Eggs in each subsample were counted and the mean number per weight calculated for each subsample. Egg production, F, was estimated by the calculation

$$(TW \times SN) / (SW),$$

where TW = total weight of gonads;
SN = mean subsample egg number; and
SW = subsample weight.

Results

Age and growth

For each species, the von Bertalanffy parameters were estimated for males and females separately, and for both sexes combined. An ANOVA was used to statistically compare the amount of variance described by both the separate and combined growth curves. ANOVA results concluded that for both grass rockfish (F=1.16, P>0.05) and brown rockfish (F=1.15, P>0.05) there was no significant difference in the amount of variance explained by estimating sex-specific values for the three parameters. Thus, for each species growth of both sexes is adequately depicted by a single growth curve.

The von Bertalanffy parameters for grass rockfish were L_∞ = 51.3 cm, k= 0.11, t_0 = –2.41 (Fig. 1) and for brown rockfish L_∞ = 51.4 cm, k = 0.16, t_0 = –0.55 (Fig. 1). As with other rockfishes, immature fishes grew relatively rapidly slowly as they matured. Within each species, sexes appeared to have similar life spans. The oldest male grass rockfish was 22 yr, the oldest female 23 yr. Male brown rockfish lived to 18 yr, females to 20 yr.

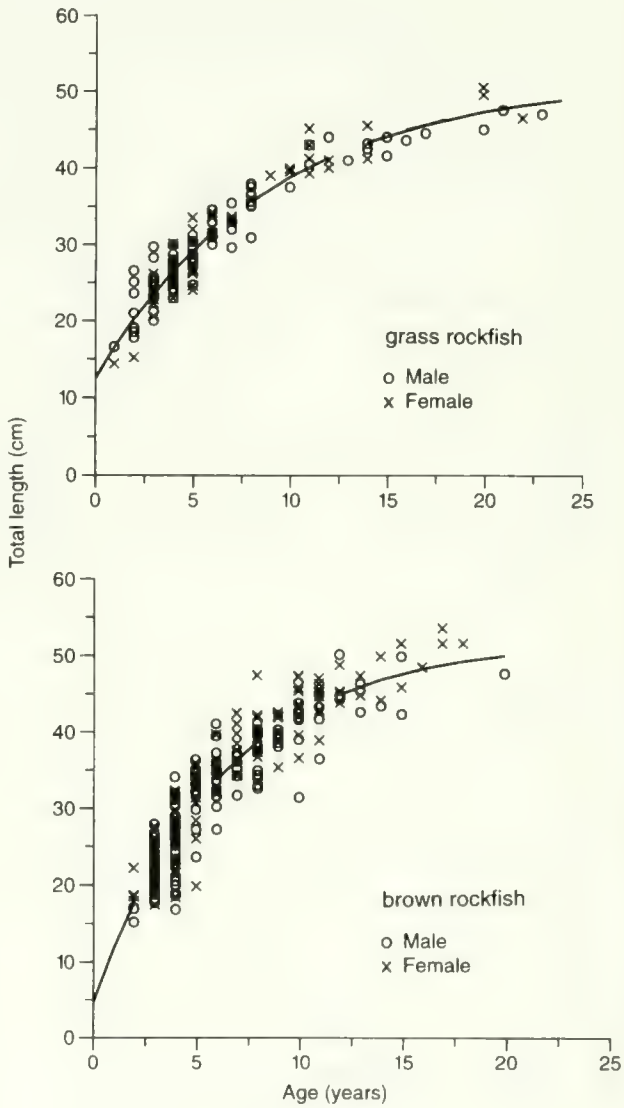

Figure 1
Von Bertalanffy growth curves for grass rockfish (*S. rastrelliger*) and brown rockfish (*Sebastes auriculatus*) from southern California.

Length-weight relationships

For both species, the relationship between total length and weight fitted the relationship

$$W = aL^b,$$

where W = weight in grams;
L = total length in centimeters; and
a and b = constants.

Parameters were estimated with Fishparm v. 3.0 (Saila et al. 1988) by using Marquardt's algorithm for nonlinear least squares parameter estimation.

To test for differences in the relationships between sexes, male and female data within a species were modeled separately. Each relationship was then $\log_{10}$-transformed to create a linear equation, and slopes of the male and female models were compared by using Student's t-test. This process was repeated with gonad weight subtracted from total body weight, to

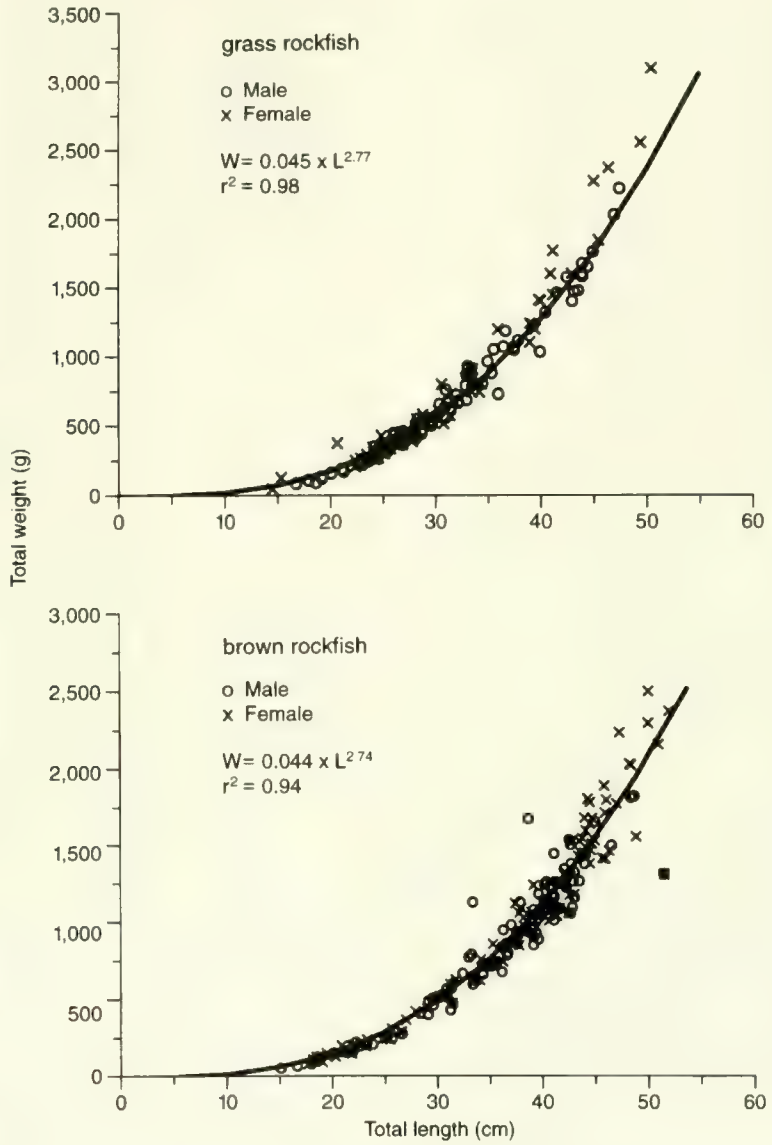

Figure 2

Length-weight relationships for grass rockfish (*S. rastrelliger*) and brown rockfish (*Sebastes auriculatus*) from southern California.

determine if any difference was simply an artifact caused by the larger female gonads.

For grass rockfish, 86 males and 73 females were measured and weighed. Although female grass rockfish tended to be heavier than males at a given length (T-test, t=2.21, P<0.05), the difference was not evident when gonad weight was subtracted from total body weight (T-test, t=1.66, P>0.05), and we therefore have combined these data into a single figure (Fig. 2).

A total of 116 male and 102 female brown rockfish were sampled. For brown rockfish, there was no significant difference in weight at a given length between males and females (T-test, t=0, P>0.05); we have also combined these data into a single figure (Fig. 2).

Length and age at first maturity

For these analyses, we examined 53 female and 64 male grass rockfish and 135 female and 129 male brown rockfish. Both male and female grass rockfish matured over relatively narrow length and age intervals (Table 1; Fig. 3). Both sexes began to mature at 22 cm and all fish were mature by 28 cm.

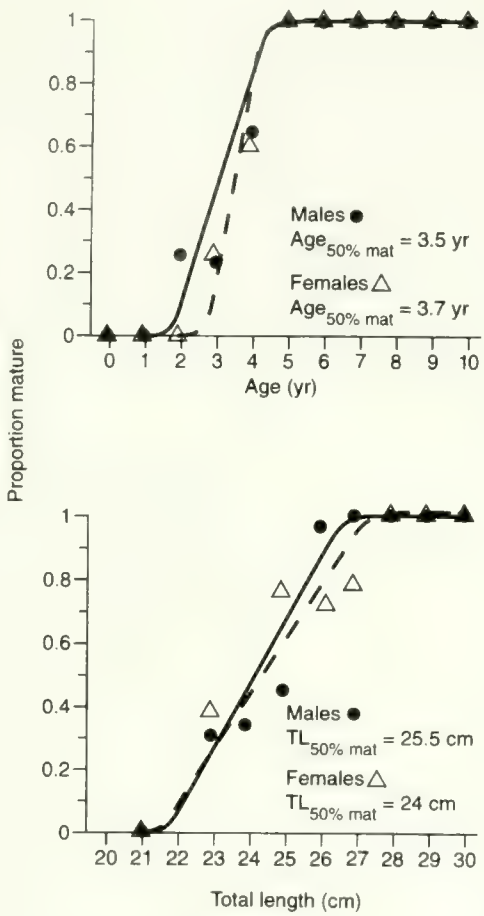

Figure 3

Age-maturity and length-maturity and relationships for male (n=88) and female (n=74) grass rockfish (*Sebastes rastrelliger*) taken in the southern California Bight, including estimated ages and lengths at which 50% of the fish were mature. Solid and dashed lines represent predicted relationship.

Fifty percent of males were mature at about 24.5 cm, and fifty percent of females at 24 cm. Male grass rockfish matured from 2 to 5 yr, females from 3 to 5 yr.

For brown rockfish, there was also little difference between sexes in either length or age at first maturity (Table 1). Males matured between 19 and 29 cm, females between 21 and 32 cm (Fig. 4). For males, 50% maturity occurred at about 25 cm, for females at 26.4 cm. Age at first maturity for both male and female brown rockfish occurred as early as 3 yr, and all fish were mature by 6 yr (Fig. 4).

Spawning seasons

Grass rockfish released larvae from January to March, reaching a peak in spawning during January (Fig. 5). Females with spawned ovaries were found only during February and March, after which followed a 6-month resting stage. Vitellogenic ovaries were common from December to February. Ovary indices remained at a minimum throughout spring, summer, and early fall, averaging about 0.3% of body weight, then increased to a peak of 6.8% in December (Fig. 6). Testes indices were also low during spring and summer (averaging less than 0.1%), rising to a peak of 0.2% in December (Fig. 6).

Brown rockfish spawned from January to August, reaching a peak in January (Fig. 5). Although females with resting stage ovaries were found from April to November, most occurred during the summer. We found vitellogenesis-stage ovaries during most months, particularly between fall and spring. For females, gonosomatic indices were lowest (averaging 0.6%) from June to November and peaked during January at 7.1% (Fig. 6). Testicular indices were lowest from March to August (averaging 0.15%) and peaked in October at 0.62% (Fig. 6).

Table 1

Maximum-likelihood estimates for the parameters of the logistic equation relating proportion mature to lengths and ages of grass and brown rockfishes. Predictive length ($l_{0.50}$) and age ($Age_{0.50}$) at 50% maturity and mean square error (MSE) of the logistic equation are also presented.

	Length			
Species	a	b	$l_{0.50}$ (cm)	r^2
Grass rockfish				
Male	0.83	20.62	24.5	0.97
Female	0.73	17.49	24.0	0.97
Brown rockfish				
Male	0.38	9.47	25.0	0.85
Female	0.62	16.36	26.4	0.99
	Age			
Species	a	b	$Age_{0.50}$	r^2
Grass rockfish				
Male	1.52	5.36	3.5	0.93
Female	1.95	7.20	3.7	0.99
Brown rockfish				
Male	1.57	6.05	3.9	0.99
Female	1.79	7.51	4.2	0.99

Fecundity

The relation between grass rockfish fecundity and total length (Fig. 7) was best described by the function

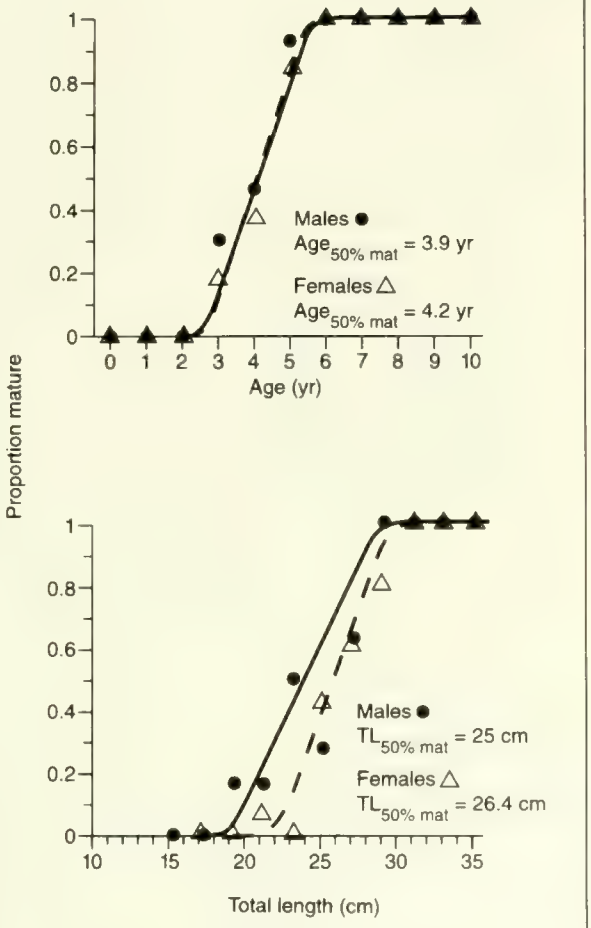

Figure 4

Age-maturity and length-maturity relationships for male (n=120) and female (n=149) brown rockfish (*Sebastes auriculatus*) taken in the southern California Bight, including estimated ages and lengths at which 50% of the fish were mature. Solid and dashed lines represent predicted relationship.

$$F = aL^b,$$

where F = number of eggs in thousands;
L = total length in centimeters; and
a and b = constants.

The value of the parameters a and b were estimated by fitting the linear function $\log F = \log a + b \log L$ by least squares. Estimated fecundity ranged from 80,000 eggs for a 26 cm TL individual to about 760,000 for one 46.5 cm long.

Discussion

In the northeast Pacific, rockfish growth rates, as measured by the term k, are quite variable (Love et al., 1990), although compared to many other groups, their growth rates are quite low (Beverton and Holt, 1960). The largest species of rockfishes tend to grow slowest (k=0.05, rougheye rockfish, *S. aleutianus*) and dwarf species exhibit relatively rapid growth (k=0.45, halfbanded rockfish, *S. semicinctus*). However, between these extremes there is no relation between maximum size and growth rate. Grass rockfish and brown rockfish growth rates are near the mean for the genus (Love et al., 1990). However, what was usual for the rockfishes was a lack of sexual dimorphism in growth rates. In most species, females grow faster than males, particularly after maturity.

Compared with most other eastern Pacific rockfishes, both species are short-lived. Of the 38 species for which we judge that fairly accurate maximum ages are known, only eight had life spans that were similar to or less than grass and brown rockfishes (Love et al.[4]). Most species lived to more than 30 years, a majority to more than 40 years. Short-lived species tend to be dwarf taxa, such as shortbelly (*S. jordani*), Puget Sound (*S. emphaeus*), squarespot (*S. hopkinsi*), and honeycomb (*S. umbrosus*) rockfishes.

For brown rockfish, there appears to be little difference in age and length at 50% maturity throughout much its range (Table 2). Although fish off central and northern California are older and larger at 50% maturity, those from Washington State and southern California are almost identical. Latitudinal differences in length or age of maturation, or both, occur in a number of rockfish species (e. g. splitnose rockfish, *S. diploproa*; widow rockfish, *S. entomelas*; yellowtail rockfish, *S. flavidus*; black rockfish, *S. melanops*; bocaccio, *S. paucispinis*) with fishes from higher latitudes generally maturing when larger or older or both (Wyllie Echeverria, 1987; Love et al., 1990; Field, 1984). However, this difference does not occur in greenstriped rockfish, *S. elongatus* (Love et al., 1990). Although it is likely that environmental parameters (e.g. water temperature, food availability, growth seasons) play a role in this phenomenon, it is not yet clear how they interact.

With 50% mature at age 4, both grass rockfish and brown rockfish mature at a young age compared with many rockfishes. Off California, most species reach 50% maturity at between 4 and 8 years (Wyllie Echeverria, 1987; Love et al., 1990); thus these two species fall in the younger part of that range. Dwarf species, such as shortbelly rockfish (*S. jordani*), Puget Sound rockfish (*S. emphaeus*) and stripetail rockfish (*S. saxicola*) mature earliest, often when 2 or 3 years old (Moulton, 1975; Wyllie Echeverria, 1987; Love et al., 1990). At the other extreme, the largest and more northerly species, such

[4] Love, M. S., M. Yoklavich, L. Thorsteinson, J. Butler. 1998. A guide to the rockfishes of the northeast Pacific. In prep.

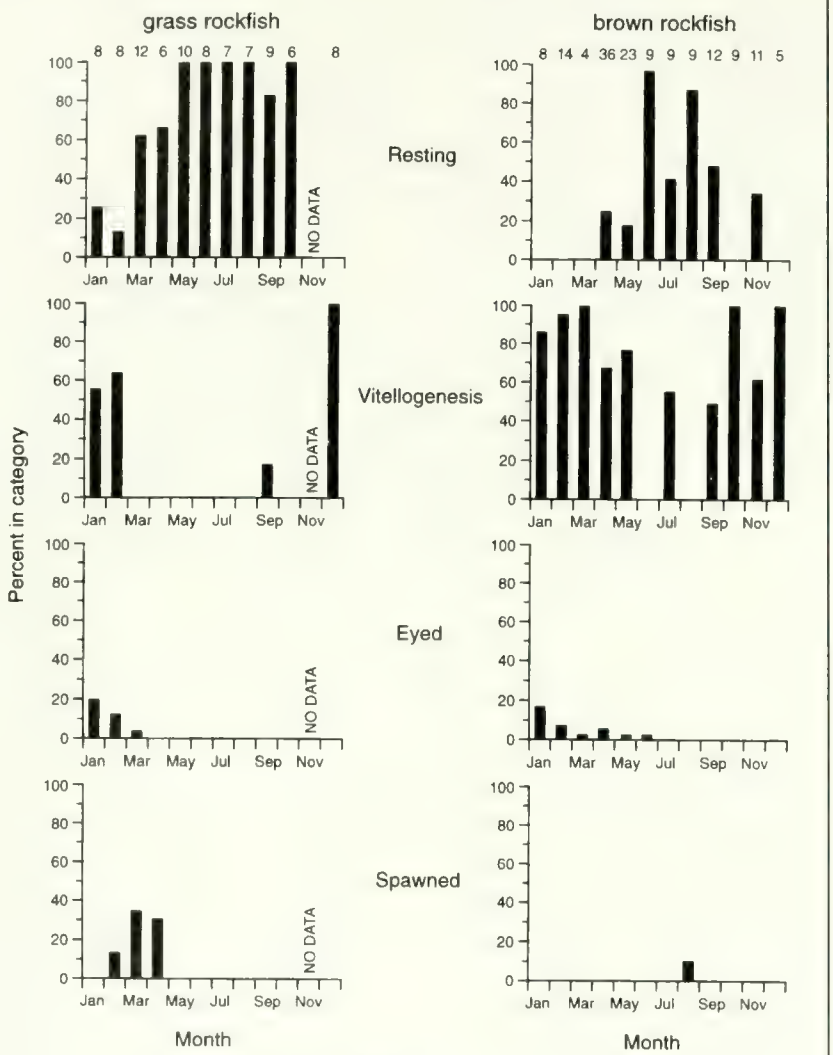

Figure 5

Percent composition by month of four gonad condition stages for female grass rockfish (*Sebastes rastrelliger*) and brown rockfish (*Sebastes auriculatus*) taken in the southern California Bight. The total number of females examined per month is listed at the top of each month in the "resting" section.

Table 2

Age and length at 50% maturity for male and female brown rockfish by area. Data from Washington State from Washington et al. (1978) and from northern-central California from Wyllie Echeverria (1987). Lengths of Washington fish are converted from fork length to total length based on Echeverria and Lenarz (1984).

Sex	Washington	Northern-central CA	Southern CA
Male	4 yr, 24 cm	5 yr, 31 cm	4 yr, 25 cm
Female	4 yr, 26 cm	5 yr, 31 cm	4 yr, 27 cm

as yelloweye rockfish (*S. ruberrimus*) and rougheye rockfish (*S. aleutianus*) may take 20 years or more to mature (McDermott, 1994; O'Connell[5]).

[5] O'Connell, T. 1994. Alaska Department of Fish and Game, 304 Lake St., Room 103, Sitka, AK 99835. Personal commun.

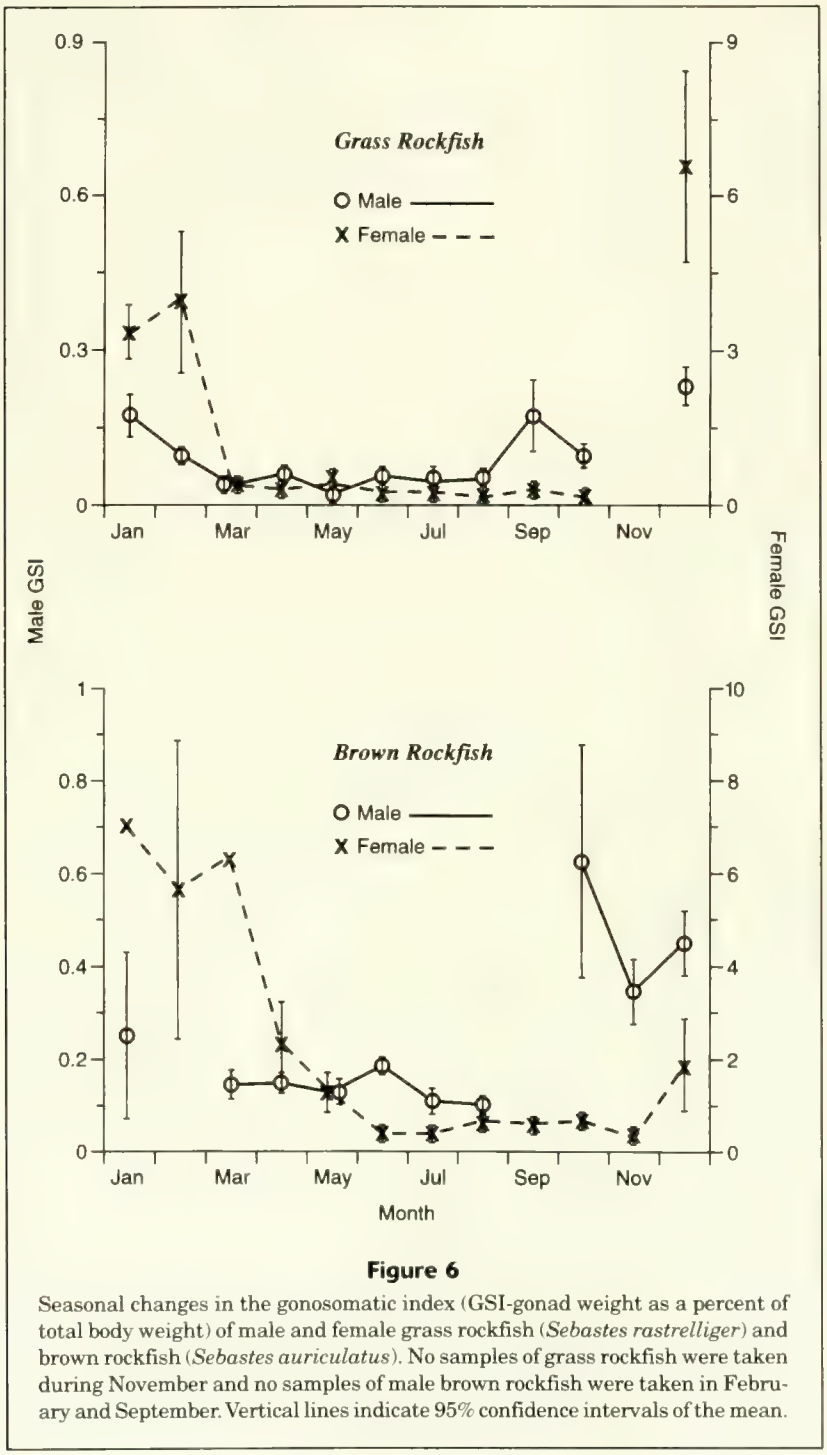

Figure 6

Seasonal changes in the gonosomatic index (GSI-gonad weight as a percent of total body weight) of male and female grass rockfish (*Sebastes rastrelliger*) and brown rockfish (*Sebastes auriculatus*). No samples of grass rockfish were taken during November and no samples of male brown rockfish were taken in February and September. Vertical lines indicate 95% confidence intervals of the mean.

Along the northeast Pacific, the vast majority of rockfish spawn in the late winter and early spring and, as with length and age at maturation, many rockfish species exhibit a latitudinal trend in spawning season. Parturition often starts earlier or is more prolonged (or both) in the southern part of a species' geographic range (O'Connell, 1987; Wyllie Echeverria, 1987; Barss, 1989; Love et al., 1990). The spawning season for brown rockfish from Puget Sound to southern California appears to follow this pattern. Spawning occurs in Puget Sound in June (Washington et al.[3]), in December–January and May–June in northern-central California (Wyllie Echeverria, 1987) and in January–August in southern California.

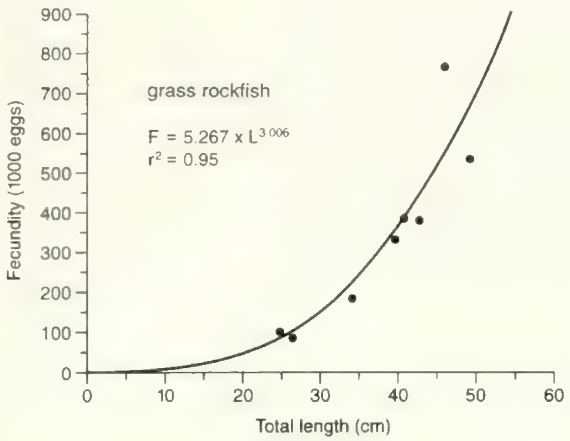

Figure 7

Fecundity-total length relationship for eight grass rockfish (*Sebastes rastrelliger*) taken in the southern California Bight.

Acknowledgments

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Abstract.—Three new species of hagfish (Myxinidae, *Eptatretus*) are described from the Galápagos Islands, Ecuador. These are the first myxinids known from this region and the first species of *Eptatretus* with five, six, and eight gill pouches reported from the eastern Pacific. A key to their identification is presented.

Three new species of hagfish (Myxinidae, *Eptatretus)* from the Galápagos Islands

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The Galápagos Islands consist of about ten principal islands and over 100 smaller ones on the equator about 500 miles off the coast of Ecuador. The biodiversity found in these islands by Darwin (1896) is also expressed in the marine fauna (McCosker, 1997); three new species of hagfish were found in only eight specimens from four trap sets (Fig. 1). An exploration off South America and the Galápagos Islands in 1891 by the U.S. Fish Commission Steamer *Albatross* reported only one species of hagfish, *Myxine circifrons* Garman (1899), taken off the Gulf of Panama. Several species of *Eptatretus* with from nine to fourteen gill pouches have since been reported from the eastern Pacific coast (Wisner and McMillan, 1990), and one species with seven gills, *E. laurahubbsae* McMillan and Wisner (1984), from the Juan Fernandez Islands, Chile. The new species described below are the first hagfish reported from the Galápagos Islands, and the first *Eptatretus* with five, six, and eight gill pouches known from the eastern Pacific. Until the formation of the Panamanian land bridge there was a long-standing connection between the Caribbean and eastern Pacific, which provided a passage for hagfish to move into the eastern Pacific from the Caribbean. These new species may be more closely related to the *Eptatretus* with five to eight gills found in the Caribbean and western Atlantic than to any currently known from the eastern Pacific. Future collecting efforts along the coast of Ecuador may reveal *Eptatretus* similar to those found off the Galápagos Islands; however, until further material is available and genetic studies are made for comparison, we can only speculate on possible origins of these Galápagos hagfishes.

Although the body color of most species of *Eptatretus* is brown to black, Fernholm (1991) described a species of *Eptatretus* on the basis of one specimen with a highly unusual pink body, stating that its color was probably caused by diet. Of the eight specimens reported here, the seven larger ones are dark purplish-brown to black or dark gray where the slime has not been removed. The smallest specimen (about 142 mm), possibly an albino, is ivory to light tan. Not enough is known about the early development of hagfish to determine if this tiny specimen would have become darker with age. Albinism has been reported by Dean (1903) and Jensen (1959), and I have collected one, an adult *E. deani* (Evermann and Goldsborough, 1907), which was pinkish-white when alive and light tan color in formalin.

Head grooves are present near the eyespots of the seven large specimens, but not on the smallest hagfish. These grooves, found in many other species of *Eptatretus* (McMillan and Wisner, 1984) and once thought similar to lateral lines,

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are now believed to have no sensory purpose. Because they are not considered a species-specific character and have no taxonomic value for the present study, they are not included in the species descriptions.

Counts of cusps and total slime pores are somewhat similar for these new *Eptatretus* species, but there are significant differences in the multicusps, numbers of gill pouches, and prebranchial slime pores which readily distinguish each of them. Some differences are found in the white patterns on the face and barbels of the seven pigmented specimens (Fig. 2), but color cannot be assigned major importance as a species character with such a small sample size.

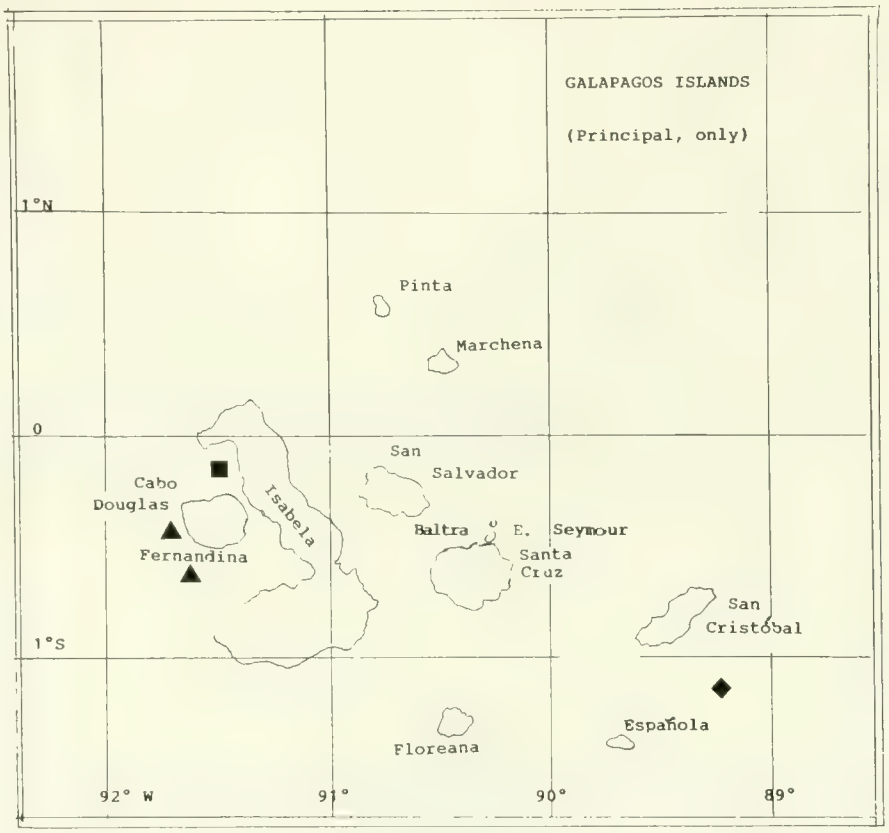

Figure 1

Principal islands of the Galápagos Archipelago, showing collection locations of the three new species of *Eptatretus*: ■ = *E. grouseri*; ◆ = *E mccoskeri*; and ▲ = *E. wisneri*.

Material and methods

All new specimens for this study were collected by John E. McCosker et al using the research submersible *Johnson Sea-link* (JSL), on the California Academy of Sciences and Harbor Branch Oceanographic Institute Galápagos Expedition during November 1995. The three new species collected by the California Academy of Sciences and described below were among eight specimens taken in four trap sets; additional specimens (nontypes) of Galápagos *Eptatretus* were given to the Instituto Nacionál de Pesca, Guayaquil, Ecuador, and were not available for study. Collection data and disposition of specimens are listed in the treatment of each new species. Institutions in which type specimens have been deposited are the California Academy of Sciences, San Francisco (CAS), United States National Museum, Washington, D.C. (USNM), and Scripps Institution of Oceanography, La Jolla, California (SIO).

McCosker[1] described the method of capture as follows: "Hagfish were collected with a small, galvanized wire commercial two-fyked minnow trap, about 30 by 50 cm, with 2 cm openings at each end. The traps were baited with fish or molluscs, or both, weighted and set with a pinger and short float line to be retrieved on the next dive [about 8 h later]; all traps were set among boulders, often on steep slopes." McCosker further reported that every set resulted in hagfish so elusive that many escaped traps during or after retrieval. Hagfish were also seen, but not taken, at 267 m off East Seymour Island, at 274 m off Isla Floreana (Charles Island), and off Isla San Salvador (James Island) at 884 m over sand bottom, at 6.54°C. Although no study material resulted from these sets, the reports furnish information on the little-known habitat of these benthic fish and indicate locations for further collecting effort.

Methods of measuring and counting follow those of McMillan and Wisner (1984) and Wisner and McMillan (1995). Counts of gill pouches (GP), gill apertures (GA), and cusps are noted for both sides, but body proportions and slime pore counts are for the left side only. Low power magnification was required to discern head grooves and fusion of multicusps. Most of the specimens are twisted and previously cut, making some measurements and counts difficult; all specimens were measured several times and averages

[1] McCosker, J. E. 1996. California Academy of Sciences, Golden Gate Park, San Francisco, CA , 94118-4599. Personal commun.

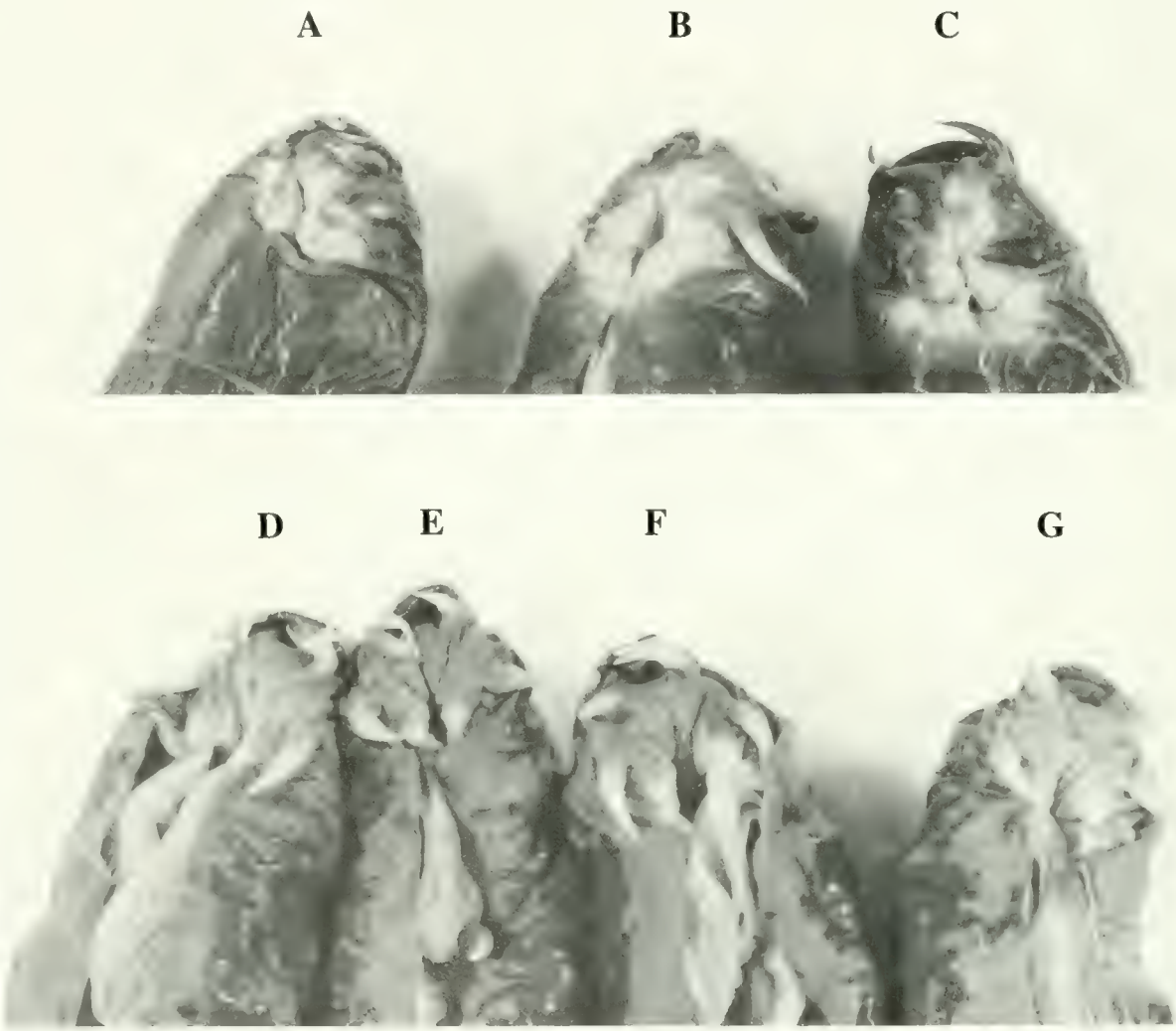

Figure 2

Frontal aspect showing pigmentation on face and barbels of three new species of *Eptatretus* from the Galápagos Islands: (**A**) holotype of *E. grouseri* (CAS 86428); (**B**) holotype of *E. wisneri* (CAS 86429); (**C**) paratype of *E. wisneri* (SIO97-76); (**D**) holotype of *E. mccoskeri* (CAS 86431); (**E**) and (**F**) paratypes of *E. mccoskeri* (SIO 97–75; and (**G**) paratype of *E. mccoskeri* (USNM 344905).

used to calculate body proportions in thousandths of total length (TL). About 6–9 mm of shrinkage was noted in the total lengths of the seven larger specimens between 24 March 1996 and 20 March 1997. Some shrinkage occurs in all specimens on preservation, mainly in the trunk length, and apparently slightly more when ethanol is the preservative used, as in this case. Selected body proportions and counts of slime pores and cusps are shown in Table 1.

Because variations in color patterns are often noted in large collections, color is not usually considered of much importance. However, the two species with eight gills have distinct differences in the white patterns on their faces and barbels that may provide a useful character in distinguishing between them. The "face" is the anteriormost part of the specimen, the ventral aspect of the head, delineated by three pairs of long, slender protruberances thought to be sensory organs and commonly referred to as barbels. The first two pairs are above and below and adjacent to the nasopharyngeal duct, which is the intake opening for water to the pharynx.

The third pair lies just outside another set of short, fleshy protruberances on each side of the mouth,

Table 1

Selected measurements and counts of slime pores and cusps of three new species of *Eptatretus* from the Galápagos Islands. Species name followed by number of specimens in parentheses; total length of holotype followed by TL of paratype(s) in parentheses; body proportions in thousandths of TL, average followed by values for all specimens.

Measurements	*E. grouseri* (2)	*E. mccoskeri* (4)	*E. wisneri* (2)
Total length in mm	380 (142)	320 (283,298,300)	360 (328)
Prebranchial length	225 (211–239)	249 (237–262)	213 (194–229)
Branchial length	71 (63–79)	97 (93–101)	105 (100–111)
Trunk length	544 (535–553)	494 (487–500)	516 (503–28)
Tail length	160 (158–162)	162 (156–177)	168 (167–171)
Body depth withVFF	58 (49–68)	100 (94–106)	88 (85,92)
Body depth without VFF	54 (42–66)	100 (94–106)	87 (85–89)
Body depth at cloaca	54 (48–61)	83 (78–88)	72 (72–73)
Tail depth	63 (63–63)	93 (87–102)	77 (76–78)
Slime pore counts (holotypye followed by paratype(s) in parentheses):			
Prebranchial pores	12 (13)	15 (14,14,14)	9 (9)
Branchial pores	4 (5)	7 (7,7,7)	7 (7)
Trunk pores	46 (44)	42 (40,40,41)	46 (47)
Tail pores	15 (14)	10 (10,11,12)	14 (13)
Total pores	77 (76)	74 (72,72,74)	76 (76)
Cusp counts, left, right (holotype followed by paratype(s) in parentheses:			
Multicusps, ant./post.	3,3/2,2	3,3/3,3	3,3/2,2
Unicusps(anterior rows)	8,9 (9,9)	10,10*(9,9–9,10)	9,9 (9,9)
Unicusps(posterior rows)	8,8 (8,8)	9,10 (9,9–9,10)	8,8 (8,8)
Total cusps	44 (44)	51 (48,50,51)	44 (44)

called "labial barbels," which are immediately adjacent to the oral opening, very similar in size and shape in all hagfish, and are not considered species signifcant. The other three pairs of long, slender barbels are usually measured, and sometimes used as a species character. Because many of the barbels on these specimens were curled and accurate measurements difficult to repeat, this character has not been included in Table 1. Multicusp pattern, and counts of GP and slime pores have proved to be more accurate and less variable intraspecifically than color or barbel size, and thus more important as species characters. The most significant features of taxonomic importance in this study are the counts of gill pouches, prebranchial slime pores, and multicusps. "First" and "last" refer to anteriormost and posteriormost, and tail pore counts are the sum of cloacal and caudal slime pores; other terms used are from Wisner and McMillan (1990, 1995). The water passes from the the nasopharygeal duct through the pharynx, through each afferent branchial duct (ABD) to the gill pouch, and exits through each efferent branchial duct (EBD) to its corresponding external opening (GA). Any excess water passes out of the body through the slightly larger duct known as the pharyngocutaneous duct (PCD), which is ordinarily confluent with, or occasionally just posterior to the last GP on the left side. The numbers of gill apertures are not shown in the table because the number of GA is normally the same as that of GP in the genus *Eptatretus*; however, GA count is given in each species description and in the key because the apertures are readily counted by external examination and thus provide a useful character for identification in the field. In most *Eptatretus,* including the three species described in the present study, the number of branchial pores is one less than the number of gill apertures,and each pore is slightly below and posterior to each GA anterior to the PCD. The next slime pore, usually found above and behind the PCD, is the first in the trunk pore series.

Key to the species of *Eptatretus* of the Galápagos Islands

1a Five or six gill pouches and apertures each side; multicusps 10 (3 in each anterior row and 2 in each posterior row) total cusps 44; prebranchial slime pores 12–13, trunk pores 44–46, tail pores 14–15, total pores 76–77 ..... ***E. grouseri,* new species**

1b Eight gill pouches and apertures each side **2**

2a Prebranchial slime pores 14–15, trunk pores 40–42, tail pores 10–12; total pores 72–74, total cusps 48–51, multicusps 12 (3 in each row); nasal barbels completely white; face mostly dark with a small white area around mouth and on labial barbels ..... ***E. mccoskeri*, new species**

2b Prebranchial slime pores 9; trunk pores 46–47, tail pores 13–14; total pores 76, total cusps 44, multicusps 10 (3 in anterior, 2 in posterior rows), nasal barbels dark with occasional white tips; face, mouth, and base of labial barbels nearly all white ..... ***E. wisneri*, new species**

Eptatretus grouseri new species

Holotype CAS 86428, female, 378 mm TL, taken at 00°14.6'S, 91°26.6'W, in a minnow trap at 2370 ft [722 m], 17 November 1995.

Paratype SIO97-77 (formerly CAS 86428), 142 mm TL, (juvenile, sex not determined), taken with the holotype.

Diagnosis Five or six gill pouches and apertures each side, last GA confluent with PCD on left side. Multicusps 3 in anterior and 2 in posterior rows, 9 unicusps in each anterior and 8 in each posterior row, total cusps 44; slime pore counts: prebranchial 12–13, branchial 4–5, trunk 44–46, tail 14–15, total slime pores 76–77; ventral finfold (VFF) vestigial, caudal finfold (CFF) well developed.

Description Both specimens have a bluntly rounded rostrum; barbels well developed, first two pairs about equal, third pair slightly longer; greatest body depth in trunk region about the same as tail depth, both only about 6 to 7 percent of TL; prebranchial length about 23 percent of TL, trunk length about 54 percent of TL. Although the two specimens differ greatly in size and color, counts of pores and cusps are very similar (Table 1). The holotype has tiny round eggs less than one mm in diameter, no ellipsoidal developing eggs and no tissue indicating previous large eggs. Body color brownish-black, head region dark brown; eye spots prominent, nearly round; face dark with small white area around mouth and on tips of barbels (Fig. 2A); VFF vestigial, with pale margin on posterior third; cloacal opening white; GA widely spaced with branchial slime pores posterior to and just slightly below each aperture; all GA on the right side and all but the second on the left side have white margins. The second gill pouch on the right side of the holotype is either undeveloped or degenerated; it appears only as thickened muscle tissue connecting the ABD from the pharynx with the EBD leading to the external GA. Only one GP lies along the tip of the dental muscle; the branchial aorta splits after the fifth (last) GP.

The paratype has six normally rounded GP on each side, the first two along the dental muscle with the aorta branching after the fifth GP. Possibly an albino, this tiny specimen is an unusual ivory to light tan body color, the prebranchial area slightly lighter with eye spots barely discernible. Also, the area around the mouth and cloaca are lighter than the body; the trunk region is just dark enough to show a white margin on the VFF. The slime pore openings are very small, but easily detected because the sacs bulge just under the thin skin.

The specimen is so young that it was not possible to determine gender even with magnification. The total cusp count only differs from that of the holotype by one, but they are very small and the multicusp fusion pattern is too indistinct to discern the number of fused cusps in the posterior rows with any certainty.

Etymology This species is dedicated to my son David "Grouser" McMillan, a Chief Engineer in the U.S. Merchant Marine, for his continued encouragement of my hagfish studies and for his knowledge and love of ships and the sea.

Distribution Known only from Galápagos Islands, Ecuador; both specimens were collected in JSL dive 3958 at 2370 ft [722 m] in Bolivar Channel, off Cabo Douglas, in a minnow trap set on a steep, sediment-laden slope of an invertebrate-rich pinnacle of pillow lava. This was the deepest set in which hagfish were collected on this expedition (Fig. 1).

Comments The body proportions differ by about two percent in prebranchial length and depth of body in trunk region, possibly because one specimen is a juvenile. Pore and cusp counts, which remain the same throughout the individual's life span, are very similar in both specimens. In this tiny paratype the first GP is about 3.5 mm in diameter, with each subsequent GP decreasing in size posteriorly until the sixth is only about 2 mm across. This difference has also been noted in size of unicusps, in which the last one is frequently much smaller at the end of each row, apparently a normal growth pattern. I have not made any study of changes in body proportions of hagfishes from juvenile to adult stage because very small specimens are seldom collected. The capture of this tiny

specimen was possible because of the use of a minnow trap with very small openings. Because of the larger openings of the myxinid traps most often used, hagfishes of less than 200 mm length are seldom caught because they escape before a trap reaches the surface.

The larger specimen with normal pigmentation has been designated as the holotype (in spite of its one abnormal GP), because its adult size allowed determination of gender and multicusp pattern, as well as more accurate measurements and slime pore counts. These two specimens are assigned to the same species because there is such close agreement in cusp and slime pore counts and most body proportion and because they were collected in the same JSL dive. A difference of one gill pouch is common in large collections of *Eptatretus* having nine or more GP, and this difference may be found occasionally in species having only five or six gill pouches. More specimens will be required to determine the usual number of GP, and whether there are enough other differences to warrant separating into two different species.

Discussion Three species of five- or six-gilled *Eptatretus* from the Caribbean Sea are *E. minor* and *E. multidens* Fernholm and Hubbs (1981), and *E. mendozai* Hensley (1985). Although these three species may have once shared a common ancestor with *E. grouseri*, they are readily distinguished by their unusual 3/3 multicusp pattern (three fused cusps on both the anterior and posterior rows of cusps). The 3/2 multicusp pattern of *E. grouseri* commonly occurs in most species of *Eptatretus:* two other five-gilled species with this pattern are *E. profundis* (Barnard, 1923) from South Africa and *E. eos* Fernholm (1991) from the Tasman Sea, the latter a distinctive pink color and possessing a tube-shaped, elongated "snout." Both of these species have about 26 prebranchial slime pores, an unusually high number for *Eptatretus* and twice as many as found in *E. grouseri.* Four species of *Eptatretus* with six gill pouches and the 3/2 multicusp pattern are *E. burgeri* (Girard, 1854) from Japan and Korea, *E. hexatrema* Barnard (1923) from South Africa, *E. longipinnis* Strahan (1975) from South Australia, and *E. chinensis* Kuo and Mok (1994) from the South China Sea. *Eptatretus burgeri* has a distinctive white middorsal line as well as notably higher prebranchial and total slime pore counts, whereas the other three species have prebranchial pore counts two to three times that of *E. grouseri.* Although the number of GP is the same, these six species are not considered closely related to *E. grouseri* because of the significant differences in prebranchial and total slime pore counts, as well as wide geographic separation.

***Eptatretus mccoskeri* new species**

Holotype CAS 86431, male, 320 mm TL, taken at 01°06.3'S, 89°06.9'W, in a minnow trap at 704 ft [215 m], 16 Nov 1995.

Paratypes All males, taken with the holotype; SIO97-75, 2(283,300 mm TL); and USNM 344905, 298 mm TL.

Diagnosis Eight gill pouches and apertures each side, last GA confluent with the PCD on the left side; 12 multicusps (3 fused cusps in each row), unicusps 36–39 (9,9 to 10,10 unicusps in each anterior and 9,9 to 9,10 in each posterior row), total cusps 48–51; total slime pores 72–74, prebranchial 14–15, branchial 7, trunk 40–42, tail 10–12. Ventral finfold absent or vestigial; caudal finfold with white margin; head slightly lighter than body color, face dark except for small white area around mouth; barbels all white (Fig. 2, D–G).

Description Body color brownish black with head region slightly lighter than body color, face dark except for small white area around the mouth; eye spots visible, but not prominent; face dark, in sharp contrast to completely white barbels; prominent white margin around CFF; rostrum bluntly rounded, nearly straight across; nasal orifice large, face wide with the distance between the pairs of barbels about equal to that of their length. First five (4–6) GP lie along the dental muscle; branchial aorta branches at the sixth or seventh GP; first GA high, series curving downward to the PCD near the ventral midline; series of prebranchial slime pores starts far forward; branchial pores are tiny and close to ventroposterior margins of each GA, trunk pore series starts above and behind the PCD, a space about 5–6 mm between last trunk pore and origin of cloaca. Prebranchial length is about one fourth of TL, trunk length about half of TL; greatest body depth in the trunk region about equal to the tail depth, both about 10 percent of TL (Table 1).

Etymology This species is dedicated to my friend John E. McCosker, Senior Scientist, California Academy of Sciences, San Francisco, California, for providing this new study material, as well as for his important contributions to marine biology.

Distribution Known only from the Galápagos Islands, Ecuador; all four specimens were taken in one dive (JSL 3936) from a minnow trap set on sand bottom at the top of a seamount southeast of Isla San Cristobal (Chatham Island) at about 215 m, the shal-

lowest set where hagfish were found on this expedition (Fig. 1).

Comments Because male hagfish rarely outnumber females in any collection, it is unusual to find that these four specimens are all males; testes are developed, but no study was done to determine presence of sperm. Although both *E. mccoskeri* and *E. wisneri* (described below) have eight GP, the pattern of three fused cusps in both anterior and posterior rows, notably higher numbers of prebranchial pores and total cusps, and the sharp contrast of white barbels against the dark face of *E. mccoskeri* readily distinguish these two species. Also, the prominent white margin around the entire caudal finfold in *E. mccoskeri* is much less apparent in *E. wisneri,* showing only as a thin white edge on the tip of the CFF. The numbers of pouches along the dental muscle and position of branching of the branchial aorta also differ slightly in these two 8-gilled species. Three other species of *Eptatretus* with 8 GP and the 3/2 multicusp pattern are listed below in the discussiom of *E. wisneri.*

Eptatretus wisneri new species

Holotype CAS 86429, female, 356 mm.TL, taken at 00°28.0'S, 91°37.2'W, from a minnow trap at 1848 ft [563 m], 14 Nov 1995, [JSL dive 3952].

Paratype SIO97-76 [formerly CAS 86430], male, 328 mm TL, taken at 00°17.5'S, 91°38.9'W, from a minnow trap at 1680 ft [512 m], 16 Nov, 1995 [JSL dive 3957].

Diagnosis Eight gills and apertures on each side, last GA on left side confluent with PCD; 10 multicusps, pattern of 3 fused cusps in each anterior row and 2 in each posterior row; unicusps 9 each anterior row and 8 each posterior row; total cusps 44; total slime pores 76, prebranchial pores 9, branchial pores 7, trunk pores 46–47, tail pores 13–14; face mostly white, including mouth and base of labial barbels; other barbels dark, with occasional white spots or tips (Fig. 2, B and C); eye spots distinct, large and irregularly shaped; VFF vestigial or absent, CFF well developed.

Description Body color brownish-black, head slightly lighter, with large, distinct eye spots; gill apertures with white margins; face nearly all white, including area around mouth and base of labial barbels; the VFF appears only as a pale line on the posterior half of the trunk region and the tip of the CFF has a thin pale margin. The first 3 gill pouches lie along the dental muscle; the branchial aorta branches after fifth GP; the prebranchial length is about 21 percent of TL, trunk length about half of TL, the greatest body depth in trunk region about equal to, or slightly more than the tail depth, both about 8 to 9 percent of TL (Table 1).

Etymology This species is named after Robert L. Wisner, my friend and associate at Scripps Institution of Oceanography, for his invaluable assistance with my myxinid research as well as his other contributions to ichthyology.

Distribution Known only from Galápagos Islands, Ecuador, these two specimens were taken by minnow trap on two different JSL dives, off Cabo Douglas, Isla Fernandina (Narborough Island), at 512 and 563 meters (Fig. 1).

Comments The holotye is a young female with round eggs of less than one mm, with no ellipsoidal oocytes and without evidence of tissue indicating previous vitellogenesis. The paratype is a male with well-developed testes, but no examination was done for the presence of sperm. One specimen is more brown than black, and the white face patterns are slightly different; also, the barbels of one specimen are partly white and more robust than those of the other (Fig. 2, B and C). These slight differences could be due to gender, although pigmentation is highly variable and sexual dimorphism has not been reported in hagfish. Barbels are seldom used as a species character because they are often curled, making accurate measurements difficult, and not reliable as a body proportion because their lengths are so small compared with TL. These two specimens have the same pattern of multicusps and unicusp counts, and slime pore counts are the same or only differ by one. Therefore, until further collecting provides more specimens for comparison, the slight differences in pigmentation patterns and size of barbels are considered insignificant, and the two specimens are described as one species.

Discussion *Eptatretus wisneri* is readily distinguished from *E. mccoskeri* because of its multicusp pattern of 3/2 (three on each anterior and two on each posterior row), lower numbers of total cusps, notably lower number of prebranchial and total slime pores, as well as the darker barbels and the white areas over most of the face. Three other eight-gilled *Eptatretus* with the 3/2 multicusp pattern are *E. octatrema* Barnard (1923) from South Africa, *E. indrambarayai* Wongratana (1983) from the Andaman Sea (N.E. Indian Ocean), and *E. okinoseanus* (Dean, 1904) from Japan). However, they are not con-

sidered closely related to *E. wisneri* because of differences in counts, the wide geographical separation, and the fact that this multicusp pattern is common to most species of *Eptatretus*.

Acknowledgments

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Chemical marking of juvenile snapper, *Pagrus auratus* (Sparidae), by incorporation of strontium into dorsal spines

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Abstract.—The aim of this project was to investigate the use of strontium as a chemical tag in the dorsal spines of the marine teleost *Pagrus auratus* that would allow the mass tagging of juvenile fish. Previous studies in which the incorporation of strontium has been experimentally manipulated for the purposes of marking have generally concentrated on freshwater and anadromous species. This is the first study to investigate the tagging of spines with strontium, the removal of which is nondestructive. Inductively coupled plasma-mass spectrometry (ICP-MS) was used to measure isotopic concentrations. The dorsal spines of juvenile *P. auratus* that had been immersed in salt water containing 0.125 g/L $SrCl_2 \cdot 6H_2O$ (5× ambient strontium) and 0.250 g/L (10× ambient) for five days incorporated ^{86}Sr at levels greater than those in control fish. The strontium signal was persistent in spines for at least 36 days and showed no sign of decay during the experiment. No effects of the treatments on fish health or growth were detected. Short-term immersion experiments (6 hours to 5 days) indicated that treatments of 10× ambient or greater for 4–5 days were required to tag fish reliably with strontium. Natural levels of strontium in the spines of juveniles varied among locations separated by tens of kilometres along the coast of New South Wales. Natural variations in strontium concentrations were not great enough, however, to obscure the differences between tagged and wild fish. It was concluded that strontium immersion is a useful and relatively environmentally safe method of tagging large numbers of small fish.

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Calcium is incorporated into the calcium carbonate matrix of otoliths and into the calcium phosphate matrix of the skeleton, spines, and scales as fish grow (Francillon-Vieillot et al., 1990). In addition to calcium, trace elements, such as strontium, are also incorporated into the calcified components of fish. The chemical similarities of Ca^{2+} and Sr^{2+} ions (i.e. similar ionic radius and identical valence) allow strontium ions to act as replacements for calcium during the process of calcification. Ca and Sr concentrations in calcified components have been explored for their relationships with variations in environmental conditions (Edmonds et al., 1989; Gallahar and Kingsford, 1992), such as temperature (Kalish, 1989; Radtke et al., 1990; Townsend et al., 1992, 1995) and salinity (Kalish, 1990; Coutant and Chen, 1993; Secor et al., 1995).

The manipulation of ambient levels of chemicals such as strontium can allow fish to be marked or tagged invisibly. The marking of skeletal structures with isotopes offers a potential method for rapid tagging of large numbers of small juvenile fish. Nonradioactive strontium has been investigated, and artificially induced strontium marks have been detected in otoliths (Brown and Harris, 1995; Mugiya and Satoh, 1995; Mugiya and Tanaka, 1995; Schroder et al., 1995, 1996; Gallahar and Kingsford, 1996), scales (Ophel and Judd, 1968; Behrens-Yamada and Mulligan, 1982; Snyder et al., 1992), vertebrae (Behrens-Yamada et al., 1979; Behrens-Yamada and Mulligan, 1982, 1987; Schroder et al., 1995), and opercular bones (Guillou and de la Noue, 1987; Schroder et al., 1995). The majority of this work, however, has been done on freshwater or anadromous species.

The species investigated in this study was the snapper or red sea bream, *Pagrus auratus* (Pisces; Sparidae). The northern hemisphere and southern hemisphere forms (previously *Pagrus major* and *Chrysophrys auratus*, respectively) are now considered to be morphometrically identical (Paulin, 1990). This highly valued commercial species supports a very well established intensive aquaculture industry in Japan (Foscarini, 1988; Davy, 1990, 1991; Fukusho, 1991) and shows good potential for aquaculture in

Australia and New Zealand (Battaglene and Bell, 1991; O'Sullivan, 1992; Treadwell et al.[1]). Commercial catch rates of snapper have been on the decline in many areas (Paul, 1982; Gilbert, 1986), and one means of increasing natural populations is by reseeding the sea with hatchery-reared larvae or juveniles. *Pagrus auratus* is one of the targets for this approach in both the northern (Smith and Hataya, 1982; Ishibasi, 1986; Matsuda, 1992) and southern (Smith and Francis[2]) hemispheres. Tagging techniques are required to measure the success of such stock enhancement measures. Very large numbers of small juveniles must be tagged in these studies, and isotope tagging may be one of the more suitable techniques.

Tagging techniques have been extensively used for research on *Pagrus auratus*. Studies involving tagging have been used to investigate migration (Crossland, 1976; Jones, 1981; Sakamoto, 1984; Kato et al., 1991), the identification of separate stocks (Sanders, 1974; Moran, 1987), growth rates (Sanders and Powell, 1979; Francis and Winstanley, 1989; Tsukamoto et al., 1989; Kato et al., 1991), fishery exploitation and resilience (Crossland, 1980), and the validation of aging with oxytetracycline (Ferrell et al., 1992; Francis et al., 1992). With the exception of fluorochrome markers, such as oxytetracycline, many conventional tagging techniques are, however, unsuitable for tagging small juveniles or are too energy intensive or expensive for the tagging of large numbers of fish.

The objective of our study was to determine whether juvenile snapper (*Pagrus auratus*) could be reliably chemically tagged by the incorporation of strontium into the dorsal spines from immersion in strontium chloride. The specific aims were as follows: 1) to investigate the persistence of chemical tags in the dorsal spines of juvenile snapper following immersion of the fish in strontium chloride; 2) to determine minimum strontium concentrations and immersion periods required for effective strontium tagging; 3) to determine the feasibility of batch tagging with different levels of strontium; and 4) to compare the levels of strontium in tagged snapper with naturally occurring levels in wild-caught snapper from different estuaries. These multiple controls were required to ensure that natural variation did not confound the identification of treated fish.

Methods

Experimental work was carried out at the New South Wales (NSW) Fisheries Brackish Water Fish Culture Research Station (BWFCRS), Port Stephens. The experimental fish were hatched on 13 November 1993 from wild parent snapper caught off Broughton Island, NSW. Rearing procedures and larval characteristics may be found in Fukuhara (1985), Lopez (1986), Pankhurst et al. (1991), Battaglene and Talbot (1992), and Kingsford and Atkinson (1994). Experimental fish were kept in 2000-litre tanks on a constant flowthrough system of biofiltered oceanic water for the first three weeks, followed by biofiltered estuarine water from Salamander Bay, Port Stephens. From 14 January 1994, 770 juvenile snapper were reserved for the experiments.

The strontium salt used was strontium chloride ($SrCl_2 \cdot 6H_2O$), a relatively cheap, nontoxic and nonradioactive chemical. Strontium is found naturally in seawater at an elemental concentration of approximately 8.1 mg/L (Horne, 1969). For simplicity the amounts of strontium chloride added to the saltwater experimental tanks are expressed as multiples of this ambient strontium concentration, as follows: 1) Sr^{2+} five times ambient = 0.125 g/L of $SrCl_2 \cdot 6H_2O$; 2) Sr^{2+} ten times ambient = 0.250 g/L of $SrCl_2 \cdot 6H_2O$; and 3) Sr^{2+} forty times ambient = 1.000 g/L of $SrCl_2 \cdot 6H_2O$. Preliminary experiments (Pollard[3]) showed increased levels of dorsal spine strontium in juvenile snapper that had been immersed in strontium chloride solution.

Experiment 1: persistence of strontium

The aim of this experiment was to determine whether the strontium marks induced in the dorsal spines of juvenile snapper were persistent over at least a 36-day period. The experiment was initiated on 22 March 1994 when the fish were 129 days old and 68 mm mean fork length (SD ±6.7 mm). The experiment consisted of Sr^{2+} five times ambient, Sr^{2+} ten times ambient, and a control, each with four replicate 100-litre tanks containing eight fish each. Two fish were sampled from each tank at zero, 12, 24, and 36 days following the termination of the five-day exposure period. For comparisons between sample times, treatments, and tanks we used a partially hierarchical three-way analysis of variance.

[1] Treadwell, R., L. McKelvie, and G. B. Maguire. 1992. Potential for Australian Aquaculture. Research Report 92.2 of the Aust. Bureau of Agricultural and Resource Economics, Canberra, Australia, 81 p.

[2] Smith, P. J., and M. P. Francis. 1991. Snapper reseeding in the Hauraki Gulf: scientific considerations. N.Z. MAF Fisheries Internal Report 172, Wellington, New Zealand, 22 p.

[3] Pollard, M. J. 1994. Chemical marking of juvenile snapper (*Pagrus auratus;* Sparidae) by the incorporation of iron and strontium in the spines, scales and otoliths. B.Sc. Hons. thesis, School of Biological Sciences, Univ. Sydney, Sydney, Australia, 119 p.

It was possible that Sr could affect fish growth. Thus, the change in mean fish weight per tank between the initial stocking of the tanks and the sampling of the fish remaining after 36 days was compared between treatments by using one-way analysis of variance.

Experiment 2: concentration and exposure period

The aim of this experiment was to investigate a range of strontium treatments and exposure periods in order to determine minimum concentrations and times required for marking the dorsal spines of juvenile snapper. It was also possible that different batches could be identified by different levels of strontium incorporation.

The experiment was initiated on 3 March 1994 when the fish were 110 days old and 64 mm mean fork length (SD ±4.1 mm). The 16 treatments comprised three strontium concentrations (Sr^{2+} five times, ten times, and forty times ambient) matched with each of five exposure periods (6, 12, 24, 36, and 48 hours) and a control treatment. Replication comprised two 100 litre tanks per treatment, each containing six fish. Snapper were sampled seven days after the termination of the chemical treatment. Statistical analysis involved comparisons between treatment concentrations, exposure periods, and tanks using an asymmetrical design analysis of variance and the Student-Newman-Keuls (SNK) multiple range test.

Strontium levels in wild fish

Juvenile *P. auratus* were caught between November 1993 and April 1994 with Opera House fish traps (100 × 80 × 60 cm, stretched mesh size 11 mm) from each of four estuarine locations around the Sydney region. From each estuary 20 fish of similar size to those used in experiments one and two were selected: those from Botany Bay had a mean fork length of 63 mm (SD ±5.9), from Port Jackson, 80 mm (SD ±9.9), from Middle Harbour, 82 mm (SD ±4.4), and from Port Hacking, 80 mm (SD ±5.6).

The main aim of this experiment was to compare naturally occurring levels of dorsal spine strontium in wild-caught juvenile snapper from multiple locations, of potentially different water chemistries, with 1) snapper immersed in Sr 40× ambient for 48 hours, and 2) snapper immersed in Sr 10× ambient for 5 days. Statistical analysis involved one-way analysis of variance and the SNK multiple range test.

Treatment of experimental fish

The experiments were undertaken in an enclosed room containing thirty-two cylindrical 100-litre fibreglass tanks, each with a 500-µm mesh filter, an aquarium air stone and a clear plastic cover. Twice daily water exchange from Salamander Bay was provided by a 1000-litre supply tank for each row of eight tanks. Photoperiod was ten hours of light per day, and tanks were cleaned weekly. Approximately 0.125 g of feed per fish per day was distributed in three equal portions throughout the day. The specially formulated dry snapper diet was a 50% protein extruded diet based on 64% fish meal, similar in composition to that in Quartararo et al. (1992). To maintain a constant stocking density, fish mortalities were compensated for by replacement with similar-size untreated snapper, fin-clipped for identification.

The water quality parameters measured every second day were pH (which averaged approximately 8.1), electrical conductivity (approx. 52 mS/cm), turbidity (generally 0 or 1 NTU), dissolved oxygen (approx. 8.6 mg/L), water temperature (approx. 19–23°C), and salinity (approx. 34.3 ppt). No significant differences were observed between tanks for any of these parameters, which remained within a range generally acceptable for the maintenance of fish health (Poxton and Allouse, 1982).

Treatments were randomly allocated to tanks. All fish chosen appeared healthy and in good condition. Wet weight and fork length were measured prior to introduction of representative groups to the experimental tanks. Sedation was necessary to allow safe handling and was achieved with 0.5 mL/L of benzocaine solution, which comprised 100 g/L ethyl p-amino benzoate ($C_9H_{11}NO_2$) in 70% ethanol solvent (Summerfelt and Smith, 1990). The fish were acclimatized to the tanks for a period of 5 days for experiment 1 and 8 days for experiment 2. Strontium treatments were initiated by dissolving the appropriate quantity of chemical salt in each tank. For the duration of the treatment there was no water exchange or cleaning activities. There was also no feeding of the fish during treatment to avoid uneven uptake of the chemical marker among individuals as a result of differential feeding (e.g. Gallahar and Kingsford, 1996). Treatment was terminated after the prescribed exposure period by allowing the exchange of new water. Fish were removed by dip net from the tanks and placed into a lethal dose of 1.0 mL/L benzocaine solution at the appropriate time of sampling, then measured, and frozen for storage.

Dorsal spine tissue samples were dissected from the treated and control snapper. Each sample consisted of four sturdy spines from the midfront of the dorsal row. The weaker posterior spines were avoided where possible. These samples were then placed into polypropylene eppendorf tubes and dried overnight in a 75°C oven. The tubes were then cooled for half

an hour prior to weighing. The tubes were sealed during this time to reduce moisture uptake which could have caused an increase in weight. Samples were weighed to the nearest 0.001 mg.

The remaining steps took place in a laminar flow cabinet to avoid contamination. With a pipette we placed 50 µL of 1% nitric acid (H_2NO_3) into the eppendorf tube containing the spines for 10 seconds and then removed the acid. This procedure cleaned possible external contaminants from the surface of the sample. The time and concentration needed for cleaning were determined by microscopic examination of the spines to check for excessive etching and loss of bone. The contents of the eppendorf tube were then dissolved in a proportional amount of 75% nitric acid to produce a standard 1 mg of spine tissue per 10 µL of solution. After allowing an hour or more for the sample to fully dissolve in the sealed tube, 10 µL of solution was removed and added to a sample tube containing 4950 µL of milliQ water and 40 µL of concentrated nitric acid. This resulted in a standardized 0.2 mg/µL sample solution in 1% nitric acid which became the sample concentration used in our experiment after preliminary analyses with ICP-MS.

Table 1

Analysis of variance for experiment 1: persistence over 36 days. Three-way partially hierarchical analysis of variance to test for differences in dorsal spine ^{86}Sr among sample times 0, 12, 24, and 36 days (fixed factor=time), treatments (treat) (Sr^{2+} zero, 5× and 10× ambient; fixed factor), and tanks (random factor). Nonsignificance at P=0.05 is indicated by n.s. Cochran's test; df = 1; no. variances (k) = 48; and C = 0.1565; variances homogeneous; no transformation.

Source	df	Mean square	F-ratio	Probability
Time	3	13699.2	6.690	<0.005
Treatment	2	568635.5	105.485	<0.001
Time × treat	6	4536.0	2.215	n.s.
Tanks (treat)	9	5390.7	2.632	<0.050
Time × tanks (treat)	27	2047.8	0.695	n.s.
Residual	48	2946.5		

Measurement of isotopes

Inductively coupled plasma-mass spectrometry (ICP-MS) was used to measure concentrations of strontium in the dorsal spine tissue. The model used was a Perkin-Elmer SCIEX ELAN 5000 with a Gilson 212B autosampler for sample introduction, and procedures were similar to those described in Dove et. al. (1996). The ICP-MS was optimized with a 0.010 mg/L standard solution covering the extremes of the mass range. By using the graphics application, we were able to adjust the nebulizer flow to maximize the ^{103}Rh signal and balance the signals for ^{24}Mg and ^{208}Pb from the standard solution. The quantitative analysis function of the ICP-MS was externally calibrated by using calibration standards with concentrations of 1, 10, 100, and 500 parts per billion, i.e. those covering the range of expected concentrations. The correlation coefficient of the calibration curve was generally 1.000 for ^{86}Sr, the isotope used for analysis. ICP-MS interferences such as isobaric overlaps or plasma-induced polyatomic ions are generally negligible for strontium. A blank solution containing only the 1% nitric acid matrix was also analyzed prior to the sample solutions, so that the isotopic concentration of the acid matrix could be subtracted.

Quality control solutions were analyzed for ^{86}Sr at the start, middle, and end of each analytical run for each date of analysis, allowing the stability of the analyte signal to be monitored both within and between runs. The quality control readings obtained were not constant over time, owing perhaps to clogged sampling cones. The results for the spine samples, therefore, required adjustment in relation to the quality control results. We assumed that there was no change in the ^{86}Sr concentration of the quality control solution over time. External drift correction can significantly improve both accuracy and precision (Jarvis et al., 1992).

Treatment of data

Data were analyzed by analysis of variance according to the general recommendations of Underwood (1981). Normality of data was tested with Cochran's test. Student-Newman-Keuls (SNK) multiple range tests were used for *a posteriori* comparisons among treatments where appropriate. Where data were missing (<2 per design), the missing values were replaced by the means for their group, and the degrees of freedom of the residual were reduced by the number of missing values.

Results

Persistence of strontium over 36 days

Differences in the ^{86}Sr concentrations of dorsal spines were found among treatments, despite differences among tanks within treatments (Table 1; Fig. 1). Fish exposed to strontium at 10× ambient incorporated more strontium into their spines than fish at 5×

ambient (SNK: Control<Sr 5× <Sr 10×). Slight fluctuations, particularly in the control and Sr 10× ambient treatments (Fig.1), caused significant differences to be found between some sampling times (Table 1), however these were not picked up by the less sensitive SNK test (0 days=36 days=12 days=24 days). The ranks of different treatments remained similar irrespective of sample time (i.e. no sample time × treatment interaction) and there was no indication of a significant decay of the strontium signal over the 36 days of the experiment. There were no significant differences between tanks within each treatment.

There were no significant differences observed among treatments for the growth of snapper as measured by the change in mean wet weight per tank between the initial stocking and sampling at 36 days (ANOVA: df=2, 9; F=3.27; P=0.086, n.s.). Mortality rates were also very low for all treatments. These results suggested that effects on health or growth from the immersion of fish in strontium were minimal.

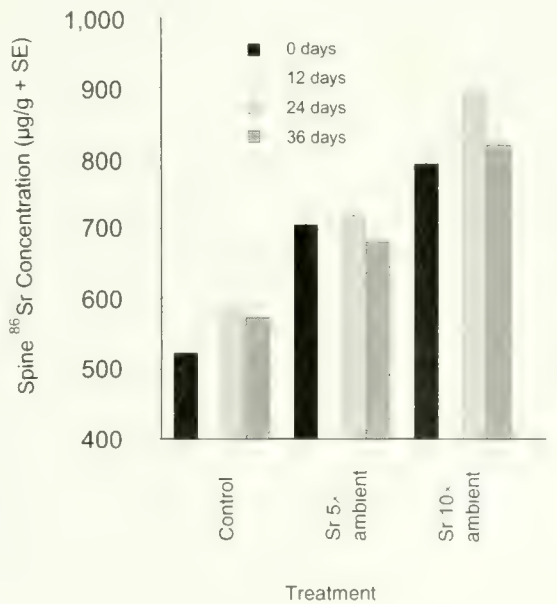

Figure 1

Persistence over 36 days of ^{86}Sr in the spines of juvenile snapper immersed in zero, 5× ambient and 10× ambient strontium for 5 days.

Strontium concentration and exposure period

^{86}Sr was incorporated rapidly into the dorsal spines of treated snapper and on average the concentrations were significantly higher in treated fish than in controls (Table 2; Fig. 2). Significant differences were found among groups of snapper treated with different $SrCl_2$ concentrations, and the magnitude of these differences varied with exposure period, resulting in a significant concentration × exposure period interaction (Table 2). Strontium incorporation increased as the exposure period increased, and the magnitude of this change was also not equal between treatments. The signals from the Sr 40× treatment were generally much greater than either of the Sr 5× or Sr 10× treatments, which were similar to one another, and the Sr 40× signal also increased much more rapidly between exposure periods (Fig. 2).

Strontium in wild fish

The experimental snapper immersed in Sr 10× for 5 days and Sr 40× for 48 hours had spine ^{86}Sr concentrations higher than those of any of the control groups (ANOVA: df=6, 105; F=70.9; P<0.001; Fig. 3), with respective concentrations 1.37 (mean 833 µg/g) and 1.55 (942 µg/g) times greater than the maximum mean concentrations of any wild fish (Port Hacking; 607 µg/g).

There were also significant differences between estuaries of origin of the wild-caught fish (ANOVA: df= 3, 74; F= 5.8; P < 0.01; Fig. 3). Fish from Botany Bay had lower levels of strontium than those from the other estuaries (SNK: Botany Bay<Port Jackson=Middle Harbour=Port Hacking). There was a 102 µg/g difference in mean spine strontium between the highest and the lowest estuary of origin. Fish from Port Jackson and Middle Harbour had intermediate values that were similar to one another. The fish used as controls during the experimental period at Port Stephens also

Table 2

Analysis of variance for experiment 2: asymmetrical design analysis of variance to test for differences in spine ^{86}Sr incorporation among treatment concentrations (conc.) (Sr^{2+} 5×, 10× and 40× ambient; fixed factor), exposure periods (exp.) (6–48 hours; random factor), and tanks (random factor). Nonsignificance at P=0.05 is indicated by n.s. Cochran's test: degrees of freedom (df) = 5; no. of variances (k) = 32; C = 0.1329; variances homogeneous; no transformation.

Source	df	Mean square	F-ratio	Probability
Concentration	2	1005648	18.167	<0.01
Exposure period	4	204047.2	163.683	<0.01
Conc. × exp.	8	55355.9	44.405	<0.01
Tanks (conc. × exp.)	15	1246.6	0.575	n.s.
Control vs. rest	1	237036.4	190.146	<0.01
Residual	150	2166.3		

had similar concentrations to the wild-caught control fish.

Discussion

Persistence of strontium

Fish that were chemically tagged with strontium could be distinguished from control fish, and the chemical marks were persistent for at least 36 days, showing no decrease and no regular pattern of change. Although in practice the length of a tagging experiment would be likely to exceed this time frame, persistence over 36 days may indicate that the strontium signal is also likely to persist over longer periods. This conjecture, however, remains to be validated and may be dependent on factors such as bone metabolism and growth. Artificially induced strontium signals in fish scales (Ophel and Judd, 1968) and otoliths (Brown and Harris, 1995; Schroder et al., 1995, 1996) have been shown to be detectable for periods of greater than a year, and other studies investigating these components have also shown successful strontium incorporation (Table 3).

Scales (Lapi and Mulligan, 1981) and otoliths (Edmonds et al., 1989) are relatively metabolically inert tissues, and there is little biological reworking of trace elements deposited within them. On the other hand, the living cells of bone tissue may be metabolically active during growth and there may be some turnover of material over the long term. This bone remodeling is related to morphogenesis and physiological factors and involves a balance between bone resorption and bone redeposition (Francillon-Veillot et al., 1990). Nevertheless, it is likely that spines are fairly inert components of the skeleton and that active resorption is unlikely to be high, indicated by the ability to age some fish by the growth rings in spines (e.g. McFarlane and Beamish, 1987; Brennan and Cailliet, 1989; Welch et al., 1993). In addition, similar chemical processes of strontium incorporation during calcification exist between scales, otoliths, and bone, and it was expected that the incorporation of strontium into the spines would result in a relatively constant mark.

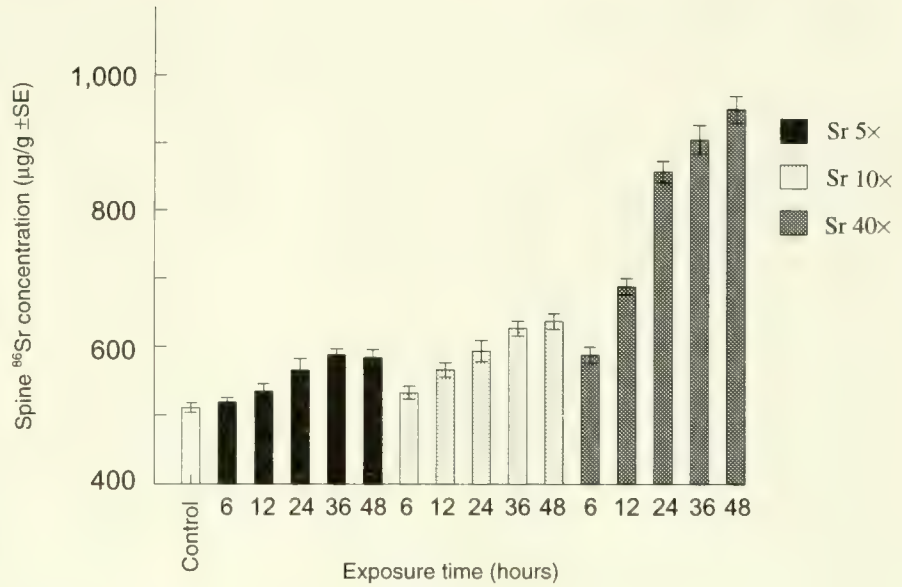

Figure 2

Differences in ^{86}Sr incorporation into the spines of juvenile snapper treated with different immersion concentrations and exposure periods.

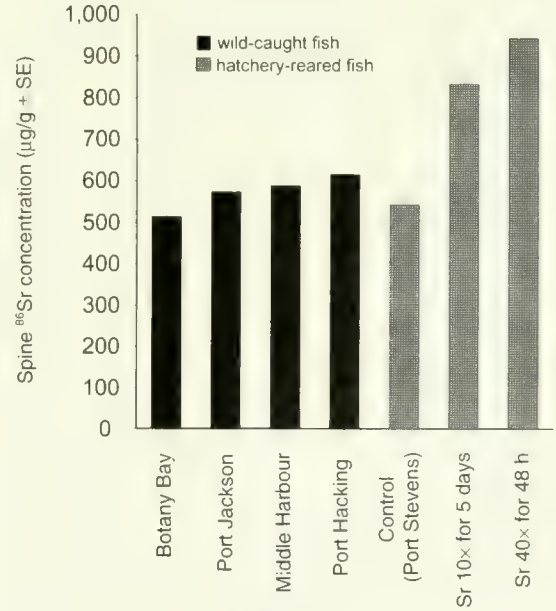

Figure 3

Naturally occurring levels of ^{86}Sr in the spines of wild *Pagrus auratus* from four estuaries in New South Wales, Australia, compared wirh those of hatchery-reared fish (controls from Port Stephens, N.S.W.) and fish treated with strontium.

Behrens-Yamada et al. (1979) found that strontium appears to become metabolically inert in the vertebrae of coho salmon, *Oncorhynchus kisutch*, after

Table 3

Comparison of previous literature in which nonradioactive strontium was incorporated into the tissues of fish for the purposes of chemical marking.

Reference	Species investigated	Aquatic medium	Method of administration	Skeletal structure	Effectiveness
This study	snapper juveniles (*Pagrus auratus*)	saltwater	immersion in 0.125g/L to 1.0 g/L Sr^{2+} (5 to 40× ambient) for 6 h to 5 days	dorsal spines	Strontium levels of greater than 10× ambient for 4–5 days produced marks which could be reliably distinguished from controls and wild snapper.
Ophel and Judd (1968)	goldfish (*Carassius auratus*)	freshwater	32 g of strontium lactate per 400 g of wet diet	scales	More than 10 times the levels of Sr in controls after one year.
Behrens-Yamada et al. (1979)	coho salmon (*Oncorhynchus kisutch*)	freshwater treatment, released into saltwater	10,000 ppm Sr introduced through the diet over 60 days	vertebrae	32 times as much Sr as controls when released; 1.4 times as much in jacks after 5 months; adults could not be distinguished.
Behrens-Yamada and Mulligan (1982)	coho salmon adults	as above	as above	core samples of scales and vertebrae	Successful identification of adults after 5 months.
Behrens-Yamada and Mulligan (1987)	coho salmon fry	freshwater	immersion in 1 µg/mL Sr for 49 days	vertebrae	Sr mark still detectable after 169 days despite dilution.
Guillou and de la Noue (1987)	brook trout (*Salvelinus fontinalis*)	freshwater	200–3200 µg/g Sr^{2+} introduced through the diet for 4 and 6 weeks	opercular bones	Able to distinguish between marked and unmarked fish at the lowest levels of ingested Sr.
Snyder et al. (1992)	rainbow trout (*Oncorhynchus mykiss*)	freshwater	immersion in 1.8, 3.6 and 5.4 mg/L Sr for 30 days and 60 days	scales	A twofold increase in exposure period and a two- or threefold increase in immersion concentration produced corresponding two- and threefold increases in incorporation.
Brown and Harris (1995)	golden perch (*Macquaria ambigua*) and trout cod (*Maccullochella macquariensis*)	freshwater	immersion in 1–20 g/L $SrCl_2$ for one to four days	otoliths	Still able to distinguish after 12 months. No measurable growth, health, or mortality effects.
Mugiya and Tanaka (1995)	goldfish (*Carassius auratus*)	freshwater	immersion in 0.1, 1.0, and 10.0 mg/L Sr for 88 days	otoliths, ribs, and scales	Strontium in otoliths remained after 92 days, whereas that in scales and ribs decreased.
Schroder et al. (1995)	chum (*Oncorhynchus keta*) and sockeye salmon (*O. nerka*) fry	freshwater	immersion in 120, 1200 and 9000 ppm $SrCl_2$ for 24 hours	otoliths, vertebrae and opercula	Able to distinguish after 34 days, and after 21 months in otoliths of fish immersed in 5000 ppm for 24 hours.
Schroder et al. (1996)	salmon fry	freshwater	immersion in 9000 ppm $SrCl_2$ for 12 hours or less	otoliths	Fish held for as little as 30 minutes in 9000 ppm were distinguishable for up to 2 years.
Gallahar and Kingsford (1996)	rock blackfish (*Girella elevata*)	saltwater	immersion in $SrCl_2$ 2.5× ambient	otoliths	Able to distinguish between marked fish and controls.

incorporation. Their inability to identify strontium-marked adults in following years was attributed entirely to dilution caused by the growth of vertebrae, rather than a process of leaching from the tissue. Behrens-Yamada and Mulligan (1982) found that the use of smaller vertebral core samples allowed the identification of strontium-labelled adult salmon. The limiting core diameter was related to the vertebral diameter of the juvenile salmon at the time of treatment.

Similarly, the growth of juvenile snapper spines will cause a dilution of the strontium signal. The ratio of marked to unmarked spine matrix will decrease as the spine enlarges. Spine growth occurs from the base upwards (e.g. McFarlane and Beamish, 1987), and the strontium mark may remain only in the upper regions as spine elongation and enlargement occurs. Only the uppermost section of the spine, corresponding to the length of the spine at the age of incorporation, should be sampled in large fish; this will result in a proportional increase in the amount of strontium in the sample.

Papadopoulou et al. (1980) found that a range of chemical constituents in the otoliths of the mackerel *Scomber japonicus colias* decreased with age. Dilution from growth, dietary changes with age, and otolith compositional changes were mentioned as possible causes. Nevertheless, the duration of most tagging experiments does not generally exceed a period of several years, and growth or age-related problems are unlikely to be a major concern over such time scales. The differences between the strontium-tagged and wild fish are great enough for there to be little confusion between the two groups if samples are taken from the uppermost spine region and tagging experiments are not designed to extend over the very long term.

Strontium in tagged and wild fish

It was a major concern for our study that naturally occurring variation in the levels of strontium in wild fish might obscure the strontium signal in fish that had been tagged by immersion in $SrCl_2$. Adult snapper may undertake movements associated with feeding or spawning (Crossland, 1976), extending the range of water chemistries experienced by the fish. Moreover, juveniles may remain resident in shallow bays and estuaries that are subject to variable inputs of fresh water (Kingsford and Suthers, 1994) and that are likely to have differences in water chemistry.

Despite the observed variation in natural levels of strontium in wild snapper, the treatments with Sr 10× for 5 days (Fig. 3) and Sr 40× for 24 to 48 hours (Figs. 2 and 3) had unequivocally higher readings. Other treatments also had higher readings. They were, however, not considered great enough for effective tagging owing to the increased variation in spine strontium expected to result from growth factors and exposure to the variable marine environment. The minimum concentration recommended is Sr^{2+} 10× ambient, with an exposure period of at least 4–5 days at this concentration. Shorter exposure periods will require concentrations greater than Sr 10×, and snapper significantly larger than those used in our study may also require higher treatment concentrations. Although the comparisons were made with wild snapper captured within a period of six months in the general region of Sydney across a range of less than 40 km of coastline, it is unlikely that fish tagged with strontium at this recommended level would be confused with wild fish from any latitude or time.

It is not surprising to find differences in naturally occurring strontium among fish from different estuaries. For example, Edmonds et al. (1989) investigated eight elements, including strontium and found elemental compositions to be specific to the geographical origin of nonmixing populations of snapper in Western Australia. Similarly, Port Jackson, Botany Bay, and Port Hacking are distinct estuaries which would also be expected to contain nonmixing juvenile snapper populations. On the other hand, Middle Harbour is within Port Jackson, and interestingly no significant difference has been observed between these two groups.

A variety of factors influence natural variation in the Sr content of otoliths. Salinity is perhaps the strongest determinant, and analysis of strontium levels has long been used to interpret the salinity histories of anadromous or catadromous fish species (Castonguay and Fitzgerald, 1982; Coutant and Chen, 1993; Limburg, 1995; Secor et al., 1995; Pender and Griffin, 1996). Decreasing water temperature causes an increase in otolith Sr/Ca ratio, with the greatest effect occurring at low temperatures. This knowledge has been used in attempts to reconstruct temperature histories of wild fish (Radtke and Targett, 1984; Radtke et al., 1990; Townsend et al., 1989, 1992, 1995, Arai et al., 1996). It has been suggested that low temperatures may impair physiological mechanisms that exist in fish and inhibit the uptake of strontium (Kalish 1989; Townsend et al., 1992). Other environmental and biological factors that influence the natural markings of calcified structures include pH (Moreau et al., 1983; Wickins, 1984), fish age and size (Papadopoulou et al., 1980; Gauldie et al., 1995), developmental and reproductive events (Francis, 1994; Kingsford and Atkinson, 1994), physiology (Kalish, 1991), periods of stress (Townsend et al., 1992), dietary differences (Edmonds et al., 1989;

Limburg, 1995; Gallahar and Kingsford, 1996), and anthropogenic pollutants (Kalish, 1995). All of these factors may cause variation in levels of strontium in wild fish. Hence, if strontium tagging is to be successful in a region, the magnitude of natural variation should be investigated at appropriate spatial and temporal scales.

Strontium tagging has been used for freshwater and anadromous species (Table 3), but investigations of saltwater species are limited. Hurley et al. (1985) marked the statoliths of the short-finned squid *Illex illecebrosus* and Gallahar and Kingsford (1996) marked the rock blackfish *Girella elevata*. Because seawater has some 200–400 times the strontium content of freshwater (Guillou and de la Noue, 1987), the range of concentrations available for tagging (i.e. before saturation and precipitation) is reduced for marine fish. This limited our ability to batch mark separate groups of fish with different concentrations of the same element, especially considering the unknown factors affecting long-term persistence, such as dilution due to growth. Multiple immersions in strontium have, however, created multiple, discrete bands on the otoliths of salmon, allowing the production of codes for batch marking (Schroder et al., 1996). Another attractive possibility is to mark batches of fish with different combinations of several elements. A characteristic of ICP-MS analysis is the ease in identification of a number of isotopes with little corresponding increase in preparation time. Schroder et al. (1996) found that rubidium was incorporated into the calcified tissues of juvenile salmon. Caesium, which has a similar ionic radius and the same +2 valence as calcium, may also prove to be a likely candidate for consideration. Pollard[3] investigated iron chloride ($FeCl_3 \cdot 6H_2O$) together with strontium chloride, however the iron was not successfully incorporated into the dorsal spines of snapper.

Advantages, limitations, and applications of the technique

The strontium immersion technique allows hundreds of fish to be tagged in a single batch without the need for individual treatment. Other more labor intensive methods may introduce problems of stress from fish handling and are unsuitable for large numbers, especially the very large numbers involved in reseeding programs. Stock enhancement in Japanese waters exceeds 15 million juvenile snapper each year (Tsukamoto et al., 1989). Strontium tagging may be applied to very small fish and even larval fish (e.g. Behrens-Yamada and Mulligan, 1987). Fast body growth and the difficulties of attachment make the conventional tagging of small fish extremely difficult. Some alternatives to batch tagging with strontium and with comparable advantages include microwire tags (Beukers et al., 1995), thermal marking (Schroder et al., 1996), oxytetracycline (Francis et al., 1992; Lang and Buxton, 1993), alizarin complexone (Lang and Buxton, 1993; Secor and Houde, 1995) and other chemical fingerprints (e.g. Gillanders and Kingsford, 1996). It may be useful for some purposes to use a combination of techniques simultaneously.

The costs associated with the analysis of samples on ICP-MS are relatively high compared with those of many conventional tagging techniques, however they may compare favourably with the costs of some other chemical, electronic, or genetic methods of identification. The ICP-MS has very low detection limits, generally 100 to 1000 times more sensitive than inductively coupled plasma-atomic emission spectroscopy and inductively coupled plasma-atomic fluorescence spectrometry (Horlick and Shao, 1992). Sample preparation for ICP-MS is labor intensive; around 100 fish samples require up to 2 days preparation and a half day for analysis. Strontium marks however may also be detected by using other analytical techniques with lower costs, such as energy-dispersive x-ray spectrometry or wavelength dispersive spectrometry (Schroder et al., 1995). Many other analytical techniques, such as backscattered electron microscopy (e.g. Schroder et al., 1995), or laser ablation ICP-MS (e.g. Fowler et al., 1995), are also designed to measure microconstituents at specific loci across a section of calcified tissue, allowing the application of strontium marking for the validation of aging and batch marking of groups of fish.

Otoliths are commonly used for chemical marking and are the most widely used structures for age determination (Campana and Neilson, 1985). Otoliths comprise discrete, directly comparable samples and are recognized for their elemental stability (Edmonds et al., 1989). However, fish must be sacrificed for otolith sample collection. By contrast, spine and scale removal are nondestructive techniques, allowing catch and release techniques to be used for tagged fish. Spines are not shed or replaced during growth, unlike scales which may be lost, resorbed, or regenerated during fish ontogeny (Coutant and Chen, 1993). The small size of juvenile snapper scales also creates counting, weighing, and manipulation difficulties (Pollard[3]). The dissection of otoliths or other internal skeletal structures from large groups of fish is a labor intensive activity. The ease of removal of spines or scales allows for the routine sampling of these tissues regardless of the original purpose of fish collection. Removal for sampling could take place before the distribution of fish for commercial pur-

poses. Removal of spines or scales causes minimal physical defacement of the product, an aspect of particular relevance to the Japanese market where aesthetic appeal is highly valued.

The immersion technique for incorporation of strontium enables greater control over the degree of exposure of fish to strontium than does introduction through the diet. The latter method may introduce inconsistencies between experimental fish as a result of differential feeding, which often results from size hierarchies within the tanks (Umino et al., 1993). Intraperitoneal or intramuscular injection allows similar control of exposure to that of immersion; however each fish must be dealt with separately. Scott (1961) was unable to mark fish under 8 cm long by using injection techniques. Nevertheless, with large pelagic fish injection provides many advantages, including the ability to tag directly from the capture vessel.

The strontium tag showed no signs of decay due to leaching from the spine tissue, and tag retention times may prove to compare favorably with conventional methods. External physical tags are shed at different rates for different species, fish sizes, tag types, or attachment sites (e.g. Ingram, 1993), and may facilitate disease. Tattoos may be rendered unreadable by fish growth, and vital dyes may be leached from the animal (Laird and Stott, 1978). Clipped fins may regenerate, or there may be confusion between clipped fins and fins that have been naturally excised by predators. Population studies also assume that the proportion of tagged to untagged fish captured is representative of that existing in the population. These assumptions hold for strontium marking, whereas individuals marked with tags may be less fit for survival, more conspicuous to predators, or more likely to become entangled in capture nets.

Radioactive isotopes are effective markers of fish, as evidenced by the permanent marking of many fish by ^{14}C after atomic bomb testing in the 1950s (Kalish, 1995). A number of different radioactive isotopes have been investigated for fish tagging, for example ^{45}Ca (Bogoiavlenskaia, 1959; Anwand, 1966), ^{39}P (Karzinkin et al., 1959), ^{59}Fe (Scott, 1961), ^{137}Cs (Scott, 1962), ^{144}Ce (Hoss, 1967), ^{131}I (Fitzgerald and Keenleyside, 1978), ^{152}Eu and ^{155}Eu (Hansen and Fattah, 1986), ^{85}Sr (Carlson and Shealy, 1972; Lehtonen et al., 1992), ^{89}Sr (Farrell and Campana, 1996), and ^{90}Sr (Zhao et al., 1992). Marking with stable strontium salts however has many advantages over radioactive tagging, which is comparatively expensive, environmentally unattractive, and a potential threat to human health. The latter is an important criticism when radioisotope techniques are used to mark commercially important species, such as radioactive iridium used to tag and release snapper (Kato, 1990; Kato et al., 1991). Conversely, strontium immersion has in fact been suggested as a low-level marking technique for farm-reared brook trout destined for human consumption (Guillou and de la Noue, 1987).

A major disadvantage of the technique is that the existence of the strontium mark cannot be detected in recaptured fish prior to analysis. This means that large batches of snapper of the appropriate size may have to be analyzed when only a small proportion may be marked individuals. Most conventional tagging methods, including most radioactive isotope markers, allow *in vivo* detection of tagged fish. The number of fish requiring analysis should be minimized by the preselection of appropriate-size fish based on growth rate estimates for the appropriate geographic location (e.g. Francis and Winstanley, 1989; Tsukamoto et al., 1989; Paul, 1992). Moreover, other external features may also aid in the preselection of possibly marked fish; for example, a large proportion of hatchery-reared Japanese snapper lack an internostril epidermis (Sobajima et al., 1986). Salmon stocks of different origin have been identified by using naturally occurring differences in scale patterns (Bilton, 1972), otolith patterns (Hindar and Abee-Lund, 1992), vertebral elemental composition (Mulligan et al., 1983), or parasitic fauna (Margolis, 1963).

Stock enhancement or reseeding programmes may be of particular importance when there has been recruitment failure due to natural or anthropogenic environmental change, or as a result of overfishing. *Pagrus auratus* have been ranched and released for many years in Japan. Concerns have been raised about alterations to the gene pool from the introduction of genetically inferior cultured fish (Hindar et al., 1991; Harada, 1992). Smith and Hataya (1982) have however estimated that the release of one million snapper per year would increase annual net returns to the fishery by about 35 metric tons, and the Kagoshima Bay ranching operation appears to have become highly profitable (Matsuda, 1992). There has also been consideration of the establishment of snapper reseeding operations in the southern hemisphere (Smith and Francis[2]). Strontium tagging can assess the economic or conservation value of such stock enhancement operations and lead to refinement of the reseeding techniques, for example selection of the optimal locations and fish sizes for release. Consideration of migratory patterns (e.g. Crossland, 1976; Edmonds et al., 1989) is required to achieve spatial separation of studies, and temporal division of studies may also be achieved by the use of different cohorts separated by sufficient time to allow size separation. The success of the strontium immersion tech-

nique for *Pagrus auratus* indicates that it is probably applicable to many other saltwater fish species, and perhaps also to crustaceans and mollusks, but experimental validation would be required for each species.

Conclusions

The present study has demonstrated that the snapper *Pagrus auratus* can be reliably tagged by the incorporation of strontium into the dorsal spines. The use of strontium as a chemical marker can allow large numbers of small hatchery-bred fish to be tagged before release into the wild. Importantly, fish do not have to be sacrificed to assess whether they have been tagged. Strontium in the spines of snapper persisted for at least 36 days and there was no suggestion that the chemical signal decayed over this time. It is recommended that juvenile snapper require immersion in treatments of strontium chloride greater than 0.25 g/L (10× ambient) for 4 to 5 days for the production of reliable strontium marks in spines. Although natural levels of strontium in spines varied between some locations along the central coast of New South Wales, this variation was not great enough to obscure the differences between tagged and wild fish. It was concluded, therefore, that strontium immersion is a useful and relatively environmentally safe method of tagging large numbers of small snapper.

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Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996

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Abstract.—A commercially valuable trap fishery for spiny lobster (*Panulirus marginatus*) has existed in the Northwestern Hawaiian Islands since the late 1970s. Fisheries landings and research trapping show that spawning biomass and recruitment to the fishery collapsed in 1990 in the northern portion of the fishing ground and that there has been no recovery to the present, although recruitment remained strong at banks 670 km to the southeast. An advection-diffusion model is used to investigate larval transport dynamics between these two regions. The movement model is driven by geostrophic currents computed every 10 days from sea surface height obtained from TOPEX-POSEIDON satellite altimetry. The larval transport simulations indicate that even though larvae have a pelagic period of 12 months, banks differ substantially in the proportion of larvae they retain from resident spawners as well as the proportion of larvae they receive from other banks. In particular, recruitment to the northern portion of the fishing grounds is weak due to a very low local spawning biomass and a very limited contribution of larvae from the area of strong recruitment and high spawning biomass in the southeast. The results also suggest that satellite altimetry can provide useful information on physical dynamics for recruitment studies.

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The spiny lobster, *Panulirus marginatus*, is endemic to the Hawaiian Archipelago and Johnston Atoll. The species is found throughout the archipelago and is the target of a trap fishery in the northwestern portion of the archipelago known as the Northwestern Hawaiian Islands (NWHI). From the early 1980s to 1990, the majority of fishery catches came from two banks, Necker Island and Maro Reef, located 670 km northwest of Necker Island (Fig. 1). Catches during this period averaged about 60% from Maro Reef, 40% from Necker Island. However, in 1990 there was a dramatic collapse in recruitment of 3-year-old lobsters to the fishery at Maro Reef, and other banks north of Maro; this collapse has been attributed to climate-induced change in productivity that has impacted various other trophic levels, such as sea birds, monk seals, and reef fishes (Polovina et al., 1994). After the recruitment collapse, the fishery reduced the spawning biomass to very low levels at Maro and at other northern banks, and then fishing ceased in these areas. Even with the absence of fishing at Maro for at least six years, there is still no evidence of a recovery in recruitment as indicated from a time series of the relative abundance of 3-year-olds obtained from a standardized research survey (Fig. 2). However, at Necker, 670 nmi to the southeast, the recruitment drop at the end of the 1980s was much less severe and recovery has occurred in recent years and has supported a fishery (Fig. 2). The striking differences in recruitment levels over the past seven years between the two banks raises the possibility that there is limited larval mixing between the two banks.

Current management for the lobster fishery is based on the hypothesis that recruitment to the NWHI banks comes from a well-mixed pool of larvae with contributions from the entire archipelago, and this pool of larvae oscillates seasonally along the archipelago, pushed northwest in the spring and summer with tradewind-driven Ekman transport and pushed back southeast in the fall and winter with westerly wind-driven Ekman transport (MacDonald, 1986). A genetic analysis during 1978–80 examined allozyme variation in spiny lobsters from seven banks covering a substantial spatial range of the Hawaiian Archipelago and found no evidence of genetic differentiation between banks (Shaklee and Samollow, 1984). However, a subsequent study in 1987, using a

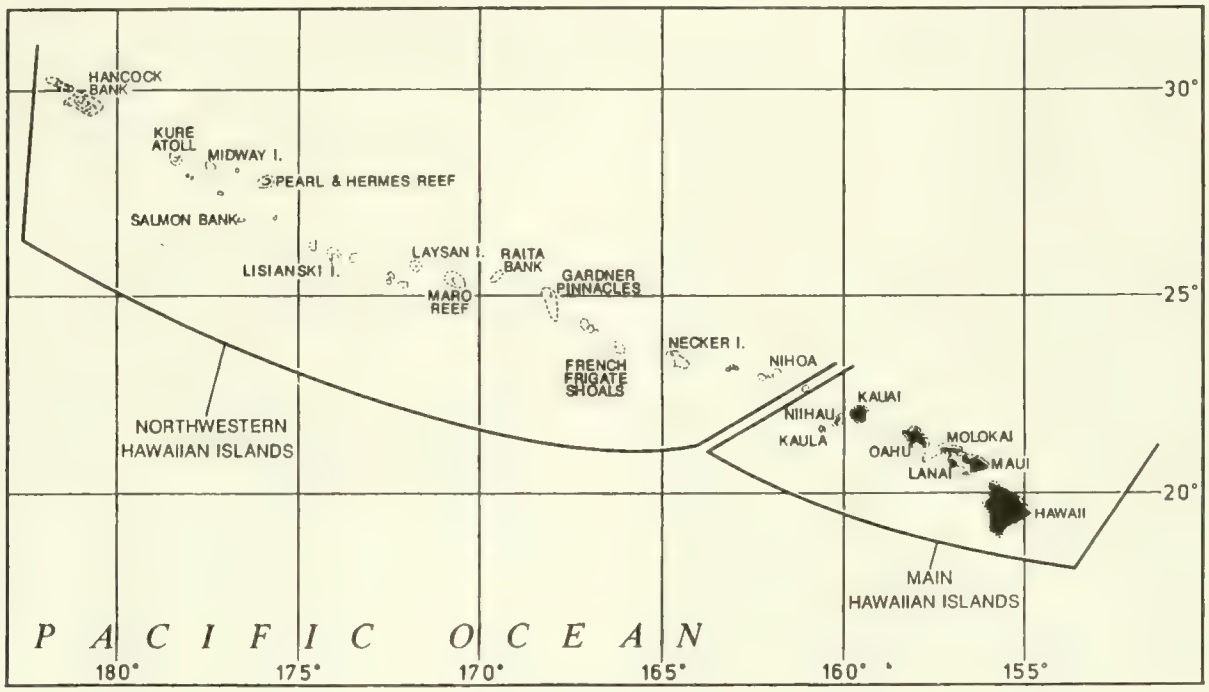


Figure 1
The Hawaiian Archipelago.

large sample size and comparing just Maro and Necker, found a statistically significant difference in allele frequency between Necker and Maro for one of the seven loci analyzed, raising the possibility that larval transport between the two banks may be limited (Seeb et. al., 1990).

The importance of Ekman transport in larval dynamics is not known, but larval sampling has found that a significant larval density exists well below the shallow Ekman layer and, in particular, that larvae appear to make diurnal movements from about 80–100 m in the day to 10–20 m at night (Polovina and Moffitt, 1995). Thus larval transport may be more influenced by transport of the mixed layer or geostrophic transport than by Ekman transport. The importance of geostrophic transport is also supported by correlations between sea-level height from tide gauges and spatial patterns in the subsequent fishery catches (Polovina and Mitchum, 1992, 1994). Indeed, the flat, leaf-like shape of spiny lobster larvae suggests they are adapted for passive horizontal transport assisted by vertical migration within the mixed layer (Lipcius and Cobb, 1994). The Hawaiian Archipelago lies near the center of the Subtropical Gyre; therefore the geostrophic transport consists of weak flow from northwest to southeast along the archipelago, turning to the east at the southern end of the archipelago. Although the mean geostrophic transport is weak, geostrophic mesoscale features, particularly eddies, are prevalent and are likely to be significant for larval spatial dynamics.

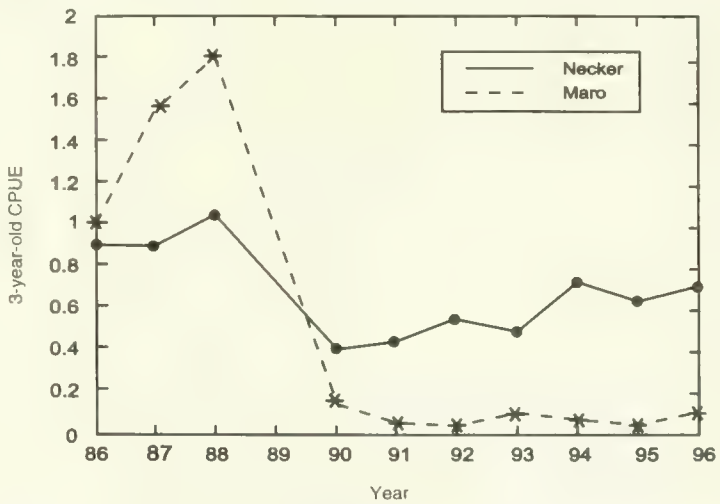


Figure 2
Standardized catch rates of age-3 spiny lobster (number of lobster per trap) from summer research cruises at Maro and Necker (data from Honolulu Laboratory, SWFSC, NMFS). No cruise conducted in 1989.

Since late 1992, data have been collected by TOPEX-POSEIDON (T-P) satellite altimetry and are available in near-real time. The satellite covers the ocean over a 10-day period, providing a temporal resolution of 10 days; however, the spatial coverage is along narrow tracks; therefore interpolation between track is required for full spatial coverage. We used this altimetry data to estimate geostrophic current and ultimately to drive a simulation model of the transport of spiny lobster larvae released from selected banks in order to describe the spatial and seasonal dynamics of larval transport. In particular, in the NWHI, the spiny lobsters spawn in the summer, during May–August, and in the winter, during November and December, and the larvae are estimated to have a pelagic duration of 12 months (Polovina and Moffitt, 1995). We investigated aspects of the spatial and temporal dynamics of spiny lobster larval transport by simulating the movement of larvae from several representative banks from summer and winter spawning over the 12-month larval duration.

Methods

Topex altimetry data

The altimetry data used in this study were obtained from a 2-day Delayed Altimeter Data project of the Laboratory for Satellite Altimetry, National Environmental Satellite, Data and Information Service (NESDIS), National Oceanic and Atmospheric Administration (NOAA), Department of Commerce. This project was a joint endeavor with the Naval Oceanographic Office (NOO) and the Jet Propulsion Laboratory (JPL). The altimetry data were first transmitted from the satellite to JPL, where the orbit position was finalized with the aid of GPS tracking data. NOO scientists performed an initial adjustment to the altimetry data using the JPL orbit information, then the data were forwarded to NOAA where a final orbit-related adjustment was made after the complete 10-day cycle of data was received. The data were aggregated into 1-degree latitude intervals along the satellite track (Fig. 3) and were expressed as a deviation from a 3-year (1993–95) mean altimetry. These data can be downloaded from an anonymous file transfer protocol (ftp) at

falcon.grdl.noaa.gov in/pub/topex_real_time

or from an internet webpage at

http://ibis.grdl.noaa.gov/SAT/near_rt/topex_2day.html.

The data were ready for public dissemination approximately 2 days after each 10-day satellite cycle was completed. Altimetry data that were not aggregated but were continuous along track lines are avail-

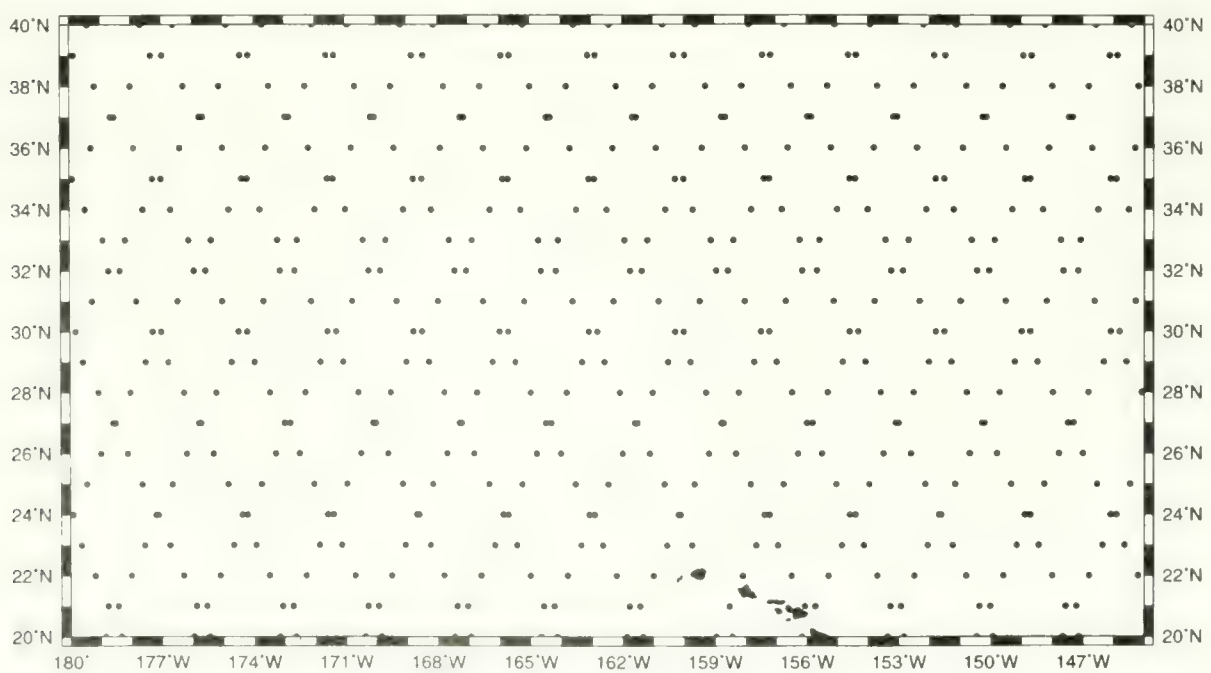


Figure 3

Spatial grid of near-real time TOPEX-POSEIDON data from a 10-day cycle.

able on CD-ROM from JPL. However, a considerable time lag may be associated with releases of these data.

After the data were downloaded, a unix shell script was used to process the individual cycle data. This script uses various subroutines of the Generic Mapping Tools (GMT) software package (the GMT software package is available from an anonymous ftp at kiawe.soest.hawaii.edu in /pub/gmt). The GMT script first smoothed and then interpolated the data using a subroutine called "nearneighbor." This subroutine placed the irregularly spaced track data onto a uniformly spaced latitude-longitude matrix, assigning values to each latitude-longitude location (node). Each node was assigned a weighted mean of all data points within a user-specified search radius (SR); i.e. a mean of all data within a geographic circle about each node. The weighting factor was a function of radial distance from the node such that $w(r) = 1/(1 + (3r/SR)^2)$, hence $w(r)$ ranged nonlinearly from 1 at the node (r=0) to 0.1 at SR units from the node (r=SR). When all orbital passes of the satellite cycle were complete, a SR value of 3 degrees could adequately interpolate regions between passes, independent of the relative date of the pass within the 10-day cycle, resulting in a complete grid file. For cycles with missing passes, the SR was able to be increased accordingly. The SR could also be specified as an absolute distance to ensure that the smoothing region was circular and not ovoid. After the deviation data were assembled on a grid, the script then added these data to another grid of equal dimensions containing the Levitus long-term mean dynamic height at 1000 m, which we assumed was representative of the mean dynamic topography for 1993–96. The Levitus data originated from the 1994 NODC World Ocean Atlas (CD-ROM data set), U.S. Department of Commerce, NOAA, National Environmental Satellite, Data, and Information Service (NESDIS). The grid file of absolute altimetry values (z) was then evaluated by the subroutine grdgradient, which calculates the east-west and north-south gradients, dz/dx and dz/dy, where x and y and z are all in centimeters. These gradients were used for calculating the u and v components of the geostrophic current as follows:

$$u = -(g/f)\frac{dz}{dy}$$

and (1)

$$v = (g/f)\frac{dz}{dx} ,$$

where g = 980 cm per second^2;
f = 2 Ω sin ϕ;
Ω = 7.29×10^{-5} radians per second (earth angular rotational velocity); and
ϕ = latitude.

These u and v values represent estimates at the surface. They can also serve as estimates of geostrophic current over the top 100-m mixed layer if integrals over the mixed layer of the horizontal density gradients are negligible. For the region of interest in our study, given the weak horizontal density gradients, the error in using these surface estimates as mixed layer estimates, according to calculations with the Levitus density field, was less than 2 cm/s. This is negligible given the time and space scales we were considering.

The u and v values were then output to an ASCII file at 0.5-degree resolution. A separate file for each 10-day period (n=169 from Oct 92 to Jun 97) was constructed for the entire Topex-Poseidon data set. The GMT script optionally produced a contour map of dynamic height with an overlay of geostrophic current vectors for each cycle. The resultant maps showed eddy and meander features that were likely important in recruitment processes (Fig. 4).

Several authors have found excellent agreement between currents estimated from T-P data and ground-truthing. Comparisons between the current estimated from satellite-tracked drogued buoys and geostrophic current estimated from T-P data in the western Pacific resulted in correlations of 0.924 for zonal velocity (u) and 0.760 for meridional velocity (v) (Yu et al., 1995). Comparisons between current speed from an acoustic Doppler current profiler along T-P track lines in the Hawaiian Archipelago agreed with estimates from T-P to within a few cm/sec (Mitchum, 1996). Sea surface height from T-P and a large set of island tide gauges, including those in the Hawaiian Archipelago, yielded a correlation of 0.66 (Mitchum, 1994).

Movement model

Individual larvae were tracked for a series of time steps starting from a given location by iteratively applying advective displacements due to water flow with additional random displacements caused by diffusion. The position of each larva was updated at each time step as follows:

$$x_{t+\Delta t} = x_t + \left[u_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] / \cos(y_t) \qquad (2)$$

$$y_{t+\Delta t} = y_t + \left[v_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] ,$$

where t = time in days;

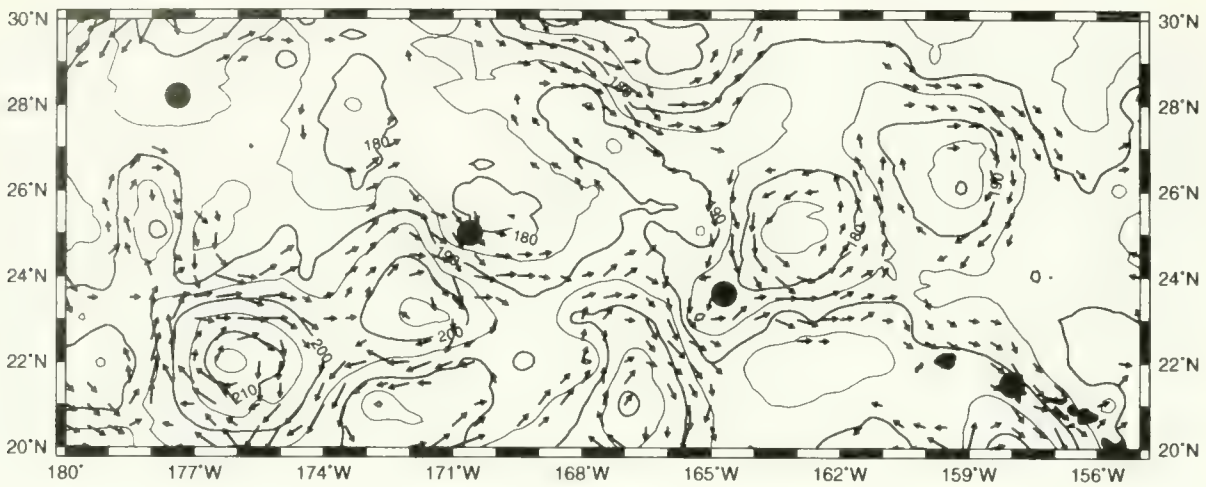


Figure 4

Sea surface height and geostrophic current estimated from a 10-day TOPEX/POSEIDON cycle, 16–26 August 1993. Only currents 8 cm/sec or larger are plotted with arrows. Solid circles from lower right (east) to upper left (west), denote Oahu, Necker, Maro, and Midway Islands, respectively.

x and y = the larval position in degrees of longitude and latitude respectively;

u and v = longitudinal and latitudinal components of velocity in degrees/day;

ε = a normal (mean 0, standard deviation 1) random variate; and

D = the eddy diffusion rate in units of degree^2/day (1 m^2/sec = 7×10^{-6} degree^2/day).

The first term in brackets in each equation is advective displacement and the second term, diffusional displacement. The cosine function in the longitudinal movement equation corrects for the fact that distance per degree of longitude decreases from the equator to the poles.

Values of u and v at particular locations and times were obtained by linear interpolation from the precalculated 0.5 degree by 10-day grid of u and v values computed from the T-P data. The time step was set to one day (Δt=1) with 365 iterations for one year of simulation. The 1-day time step was used to match the spatial resolution of the velocity field, but simulations showed that the choice of time step was robust up to about two weeks. Larvae dispersed in the model because a different diffusional displacement (a different ε) was chosen for each larva at each time step. Once larvae were even slightly separated, dispersal was further advanced because the larvae experienced different advective displacements as u and v varied spatially.

Simulations

Although lobsters presumably spawn on all banks in the Hawaiian Archipelago, for simplicity, the simulations released larvae from only four banks: Midway and Oahu (chosen as representative of the northwestern and southeastern ends of the archipelago) and Necker and Maro (representative of the main fishing banks [Fig. 1]). Each simulation released 5000 larvae at the beginning of the month from each of the four banks for the four months of the summer spawning season and the two months of the winter spawning season from 1993 to 1995. The simulations tracked the positions of all released larvae for 365 days; no larval mortality was assumed. For example, Figure 5 shows the distribution of simulated larvae 180 and 365 days after release at Maro Reef in July 1995. The distribution showed patchiness caused by underlying oceanographic features and expanded spatially over time. This simulation was based on an eddy diffusion rate of 1000 m^2/sec, and the same simulation, but with the diffusion rate reduced to 100 m^2/sec, showed a striking increase in patchiness and the same general dispersal (Fig. 6). The eddy diffusion rate for the NWHI is not known, but a range from 100 m^2/sec to 1000 m^2/sec has been proposed for another large archipelago, the Great Barrier Reef (Gabric and Parslow, 1994). Because the level of diffusion rate impacts larval patchiness and because we had a measure of actual larvae patchiness from numerous larval tows throughout the archipelago (Polovina and Moffitt, 1995), we decided the appropriate level for eddy diffusion rate by comparing the frequency distribution of larvae sampled in actual larval tows with the frequency distribution of larvae from line transects and the simulated spatial patterns for different eddy diffusion-rate values. The frequency distribution from transects with an eddy

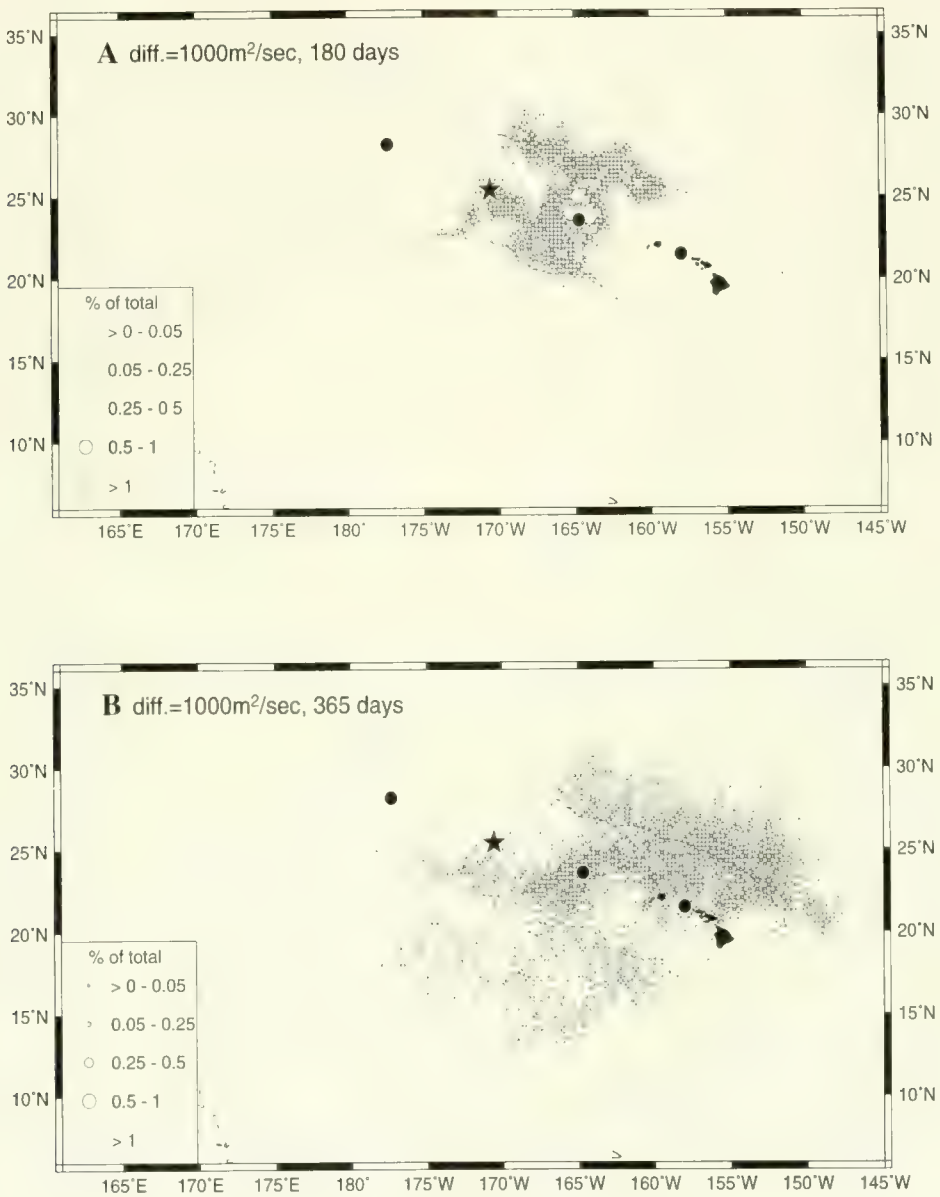


Figure 5

Simulated spatial distribution of 5000 larvae (**A**) 180 and (**B**) 365 days after release on 1 July 1995 at Maro with an eddy diffusion rate of 1000 m^2/sec. Solid circles denote Oahu, Necker, and Midway Islands, and the star marks Maro Island.

diffusion rate of 1000 m^2/sec had a lognormal distribution but underrepresented the heavy tails of the actual larval-tow frequency distribution. The frequency distribution from transects with an eddy diffusion rate of 100 m^2/sec had extremely heavy tails, in fact bimodal distribution. Either very few larvae were encountered or many larvae were encountered, resulting in a distribution that had too many large clumps compared with the observed distribution. However, an eddy diffusion rate of 500 m^2/sec produced a larval frequency distribution that closely matched the distribution from the larval tows, and this value was used in all subsequent simulations.

At the end of their larval period, spiny lobster larvae metamorphose into pueruli that, at least for other spiny lobster species, are capable of directed horizontal swimming over 40–60 km (Pearce and Phillips, 1994). For *P. marginatus*, it is not known how close a larva needs to be to a bank at the end of its larval period to recruit to that bank. The 200-m isobath around the islands and banks of the archipelago is generally circular and marks the points at

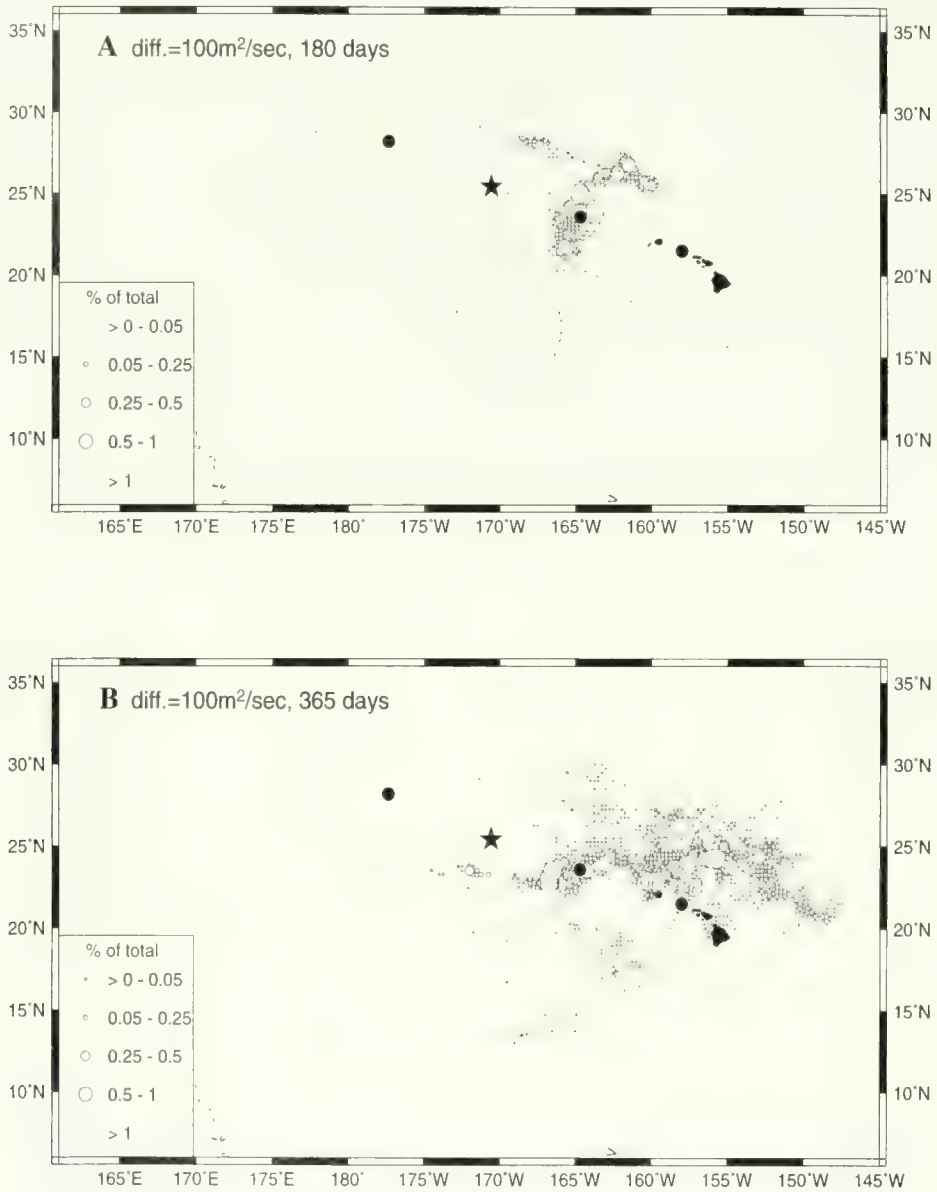


Figure 6

Simulated spatial distribution of 5000 larvae (**A**) 180 and (**B**) 360 days after release on 1 July 995 at Maro with an eddy diffusion rate of 100 m^2/sec. Solid circles denote Oahu, Necker, and Midway Islands, and the star marks Maro Island.

which the topography drops steeply to midocean depths. For Necker, Maro, and Oahu, the radius of the 200-m isobath is about 70 km. Oceanographic features resulting from interactions with topography that larvae might detect will certainly extend some distance beyond the 200-m isobath, perhaps a distance equal to the radius of the bank. Thus, as an index of larval recruitment to a bank, we assumed that larvae that were within 140 km of a bank 365 days after release would recruit to that bank. The choice of 140 km was somewhat arbitrary but because we used the index as a relative and not absolute index, the results were not particularly sensitive to this distance.

Results

Simulations were performed to describe the larval spatial dynamics from 5000 larvae released from all four banks for the 4-month summer spawning season (May–August) and the 2-month winter spawning season (November and December). The results indicated that there are spatially distinct patterns that generally persist

between years and spawning seasons and that were seen, for example, in the distribution of 1-year-old larvae in July 1995 (Fig. 7). Larvae released from Midway were advected eastward, larvae from Maro were advected east and south, larvae from Necker were advected east and south, and larvae from Oahu were advected primarily southwest (Fig. 7). A fairly persistent meander at about 26°N concentrated larvae zonally, whereas persistent westward flow at the southern end of the archipelago advected Oahu larvae westward (Fig. 7). At the center of the archipelago, specifically at Maro and Necker, a substantial portion of larvae remained close to the bank where they were spawned, even after 12 months, whereas at the ends of the archipelago, at Midway and Oahu, advection was high (Fig. 7). Further, although Necker receives abundant larvae spawned at Maro, relatively few larvae from Necker reached Maro (Fig. 7). The results, averaged over three years, showed that the percentage of larvae released at a bank and that were within 140 km of that bank 365 days later varied considerably by bank (Table 1). Differences in this percentage between winter and summer spawning seasons were not generally large but the interannual range of this percentage often varied more than threefold (Table 1). Averaged over all three years and over the two spawning seasons, the percent of larvae within 140 km of a bank 365 days after being released at that bank was 5.5%, 9.6%, 16.7%, and 16.6% for Midway, Maro, Necker, and Oahu, respectively (Table 1).

From the three years of simulations, no radical changes from the bank-specific larval distribution patterns shown in Figure 7 were seen, only spatial extensions or contractions. For example, the distribution of larvae 365 days after spawning at Necker had a northeast and southwest orientation, and larvae spawned in 1993 at Necker Island were advected east and southwest to a greater extent than larvae in 1994 or 1995 (Fig. 8).

Table 1

Mean percentage of larvae that were within 140 km of their bank of origin 365 days after release, 1993–96.

Release season	Bank	Mean percent (interannual range)
Summer	Midway	3.1 (1.8–4.7)
	Maro	10.4 (3.9–20.4)
	Necker	15.7 (9.5–20.3)
	Oahu	11.7 (8.4–15.9)
Winter	Midway	7.9 (3.7–15.0)
	Maro	8.8 (4.9–13.8)
	Necker	18.0 (8.9–29.4)
	Oahu	21.4 (12.1–33.3)

To examine the exchange of larvae between banks, the recruitment index was calculated on the basis of the bank at which the larvae originated, for both summer and winter spawning seasons, with 5000 larvae released from each bank (Table 2). The results were similar for both spawning seasons. Recruitment to Midway came almost entirely from larvae spawned at Midway. Recruitment to Maro was based largely on larvae from Maro and Midway; only 10–21% of the recruits at Maro came from Necker and Oahu. Necker had the broadest geographic source of recruits, receiving substantial larvae from all four banks. Oahu's recruits come from Maro, Necker, and Oahu (Table 2).

Discussion

The altimetry data from T-P provide a new tool to investigate recruitment questions. However, this approach has several limitations. First, because the geoid is not known, an estimate of mean dynamic topography (Levitus) was added to the T-P sea surface height anomalies. Although the accuracy of the

Table 2

Mean percentage of 12-month larvae within 140 km of each bank by bank of origin, 1993–96.

Release season	Destination bank	Bank of origin			
		Midway	Maro	Necker	Oahu
Summer	Midway	100	0	0	0
	Maro	59	31	9	1
	Necker	5	47	32	16
	Oahu	0	28	41	31
Winter	Midway	91	7	2	0
	Maro	49	30	18	3
	Necker	10	29	37	24
	Oahu	0	19	31	50

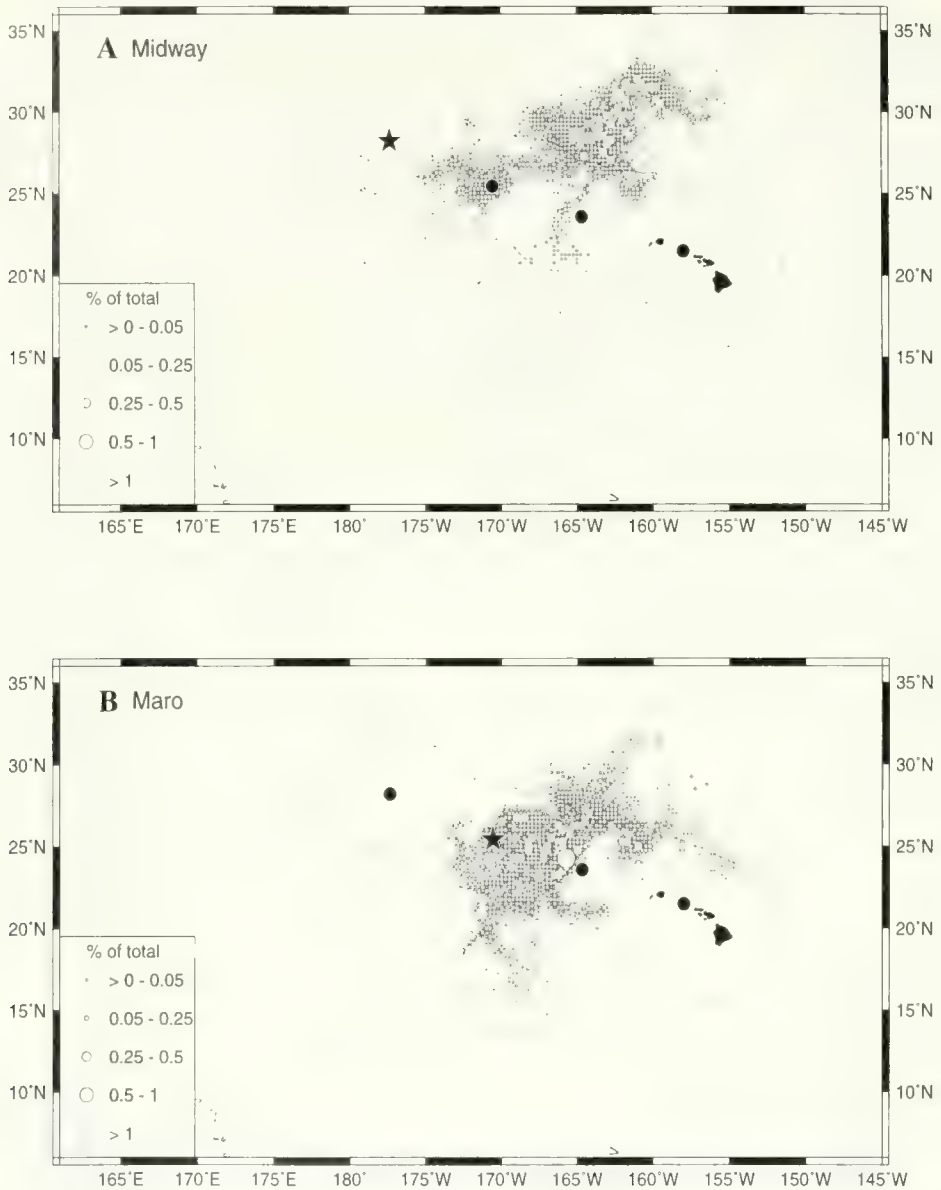
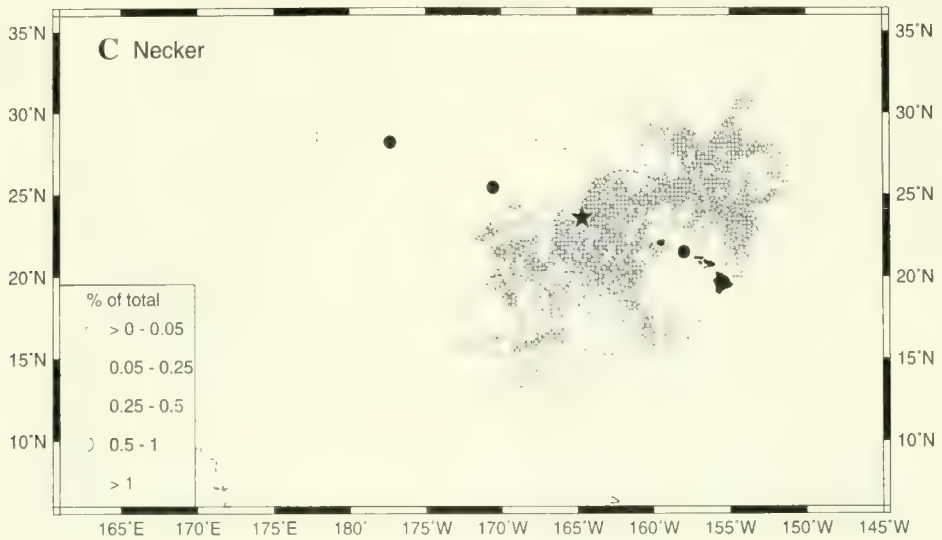


Figure 7

Simulated spatial distribution of 5000 larvae 365 days after release on 1 July 1994 at (**A**) Midway, (**B**) Maro, (**C**) Necker, and (**D**) Oahu, with an eddy diffusion rate of 500 m^2/sec. The star denotes the bank from which larvae were released. Solid circles mark the other three banks.

Levitus mean varied depending on the spatial and temporal distribution of the underlying data, it was likely that there were biases that may have had an impact on the accuracy of the estimates of absolute geostrophic current. A second limitation is that the spacing between data tracks, especially in mid- and low-latitude regions, may have been too broad to completely resolve many important finescale and mesoscale physical features. Further, this tool is appropriate only in situations where geostrophic transport is the most significant source of larval transport, situations, for example, where larvae are below the shallow Ekman layer.

In our application, this approach leads to a new hypothesis on the spatial dynamics of lobster larval recruitment in the Hawaiian Archipelago. From the simulations, we found that position of a spawning bank within the archipelago influences both the number of larvae spawned at a bank that will recruit to that bank as well as the recruitment that a bank will receive from other banks. Specifically, the results indicated that larvae are transported down the ridge from the north-



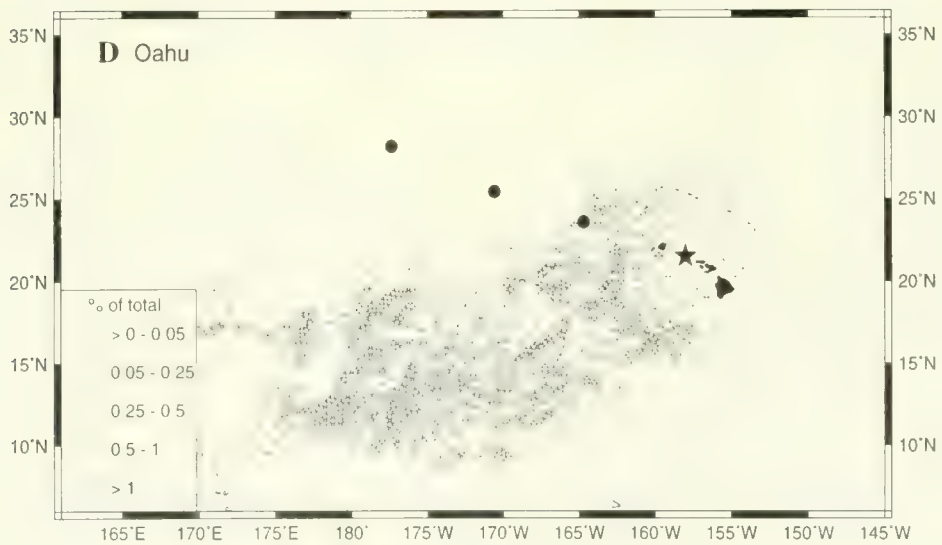


Figure 7 (continued)

west to the southeast to Necker and then southwest. Necker's persistent spiny lobster population and fishery appear to be the result of its location where it both receives larvae from banks to the northwest and southeast and also has a high retention of its own larvae. Only 670 km to the northwest, Maro's retention rate was only about one-half that of Necker, and although it contributed larvae to Necker, it did not receive any substantial contribution of larvae from Necker. This finding explains why recruitment at Maro remained depressed once the spawning biomass at Maro and other banks to the northwest were depleted, even though there was a substantial spawning biomass at Necker. However, it raises questions. Why were Maro and other northern banks so productive during the 1980s? Was the transport regime in the 1980s different, so that Maro and northern banks lost fewer larvae to the southeast and perhaps even received considerable larvae from Necker? Alternatively, because the fishery began only in the late 1970s, was recruitment always so weak at Maro and at other northern banks that the collapse at the end of the 1980s represented simply a response to overfishing an unexploited population? Although we cannot answer these questions, the results suggest that if the transport regime observed during 1993–96 persists, increased recruitment to Maro and other banks to the northwest may require an increase in the spawning population at Maro and other northern banks. Research on a similar species of spiny lobster, *P. argus*, in the Bahamas found physical trans-

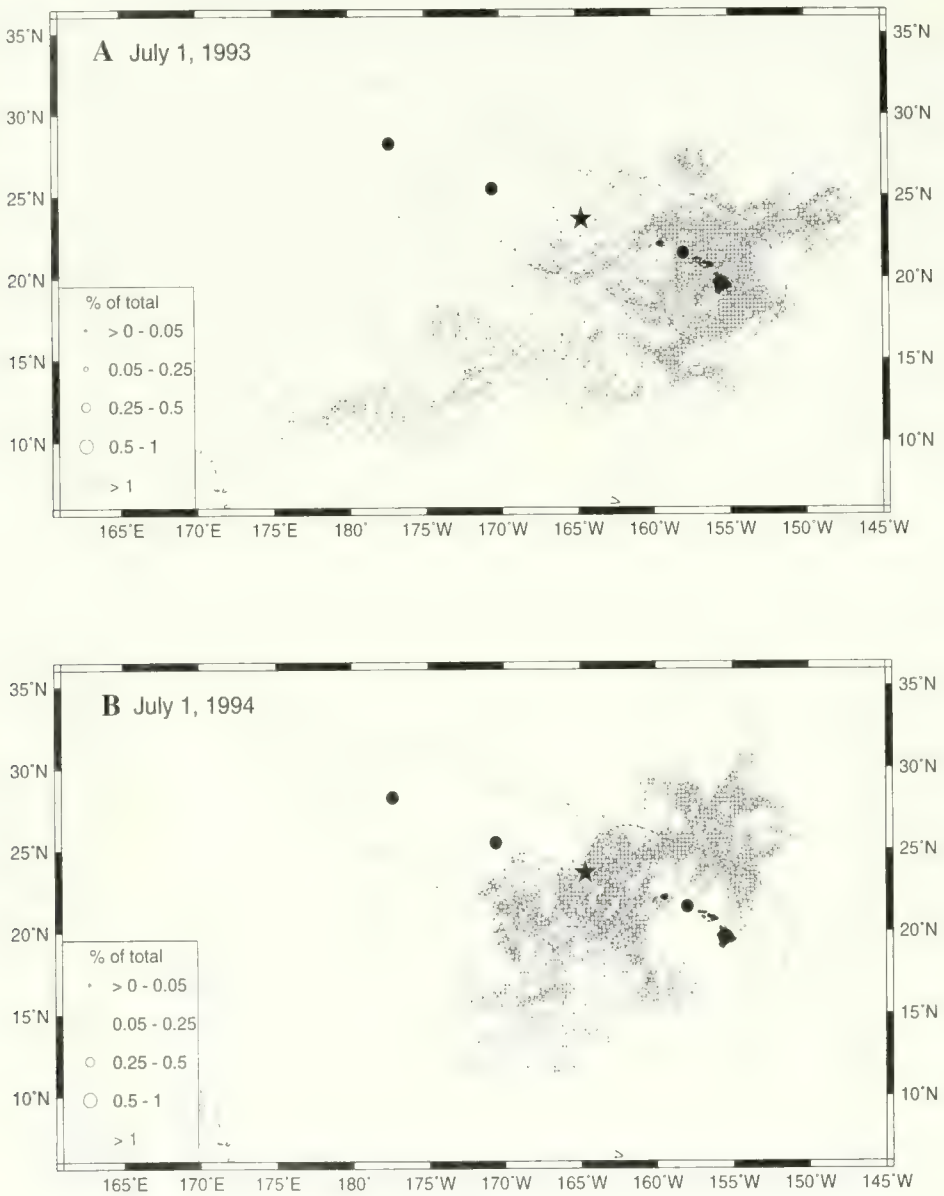


Figure 8

Simulated spatial distribution of 5000 larvae 365 days after release at Necker on (**A**) 1 July 1993, (**B**) 1 July 1994, and (**C**) 1 July 1995, with an eddy diffusion rate of 500 m^2/sec. Solid circles denote Oahu, Maro, and Midway Islands, and the star marks Necker Island.

port important to the spatial distribution of larvae (Lipcius et al., in press).

However, it is important to remember that larval abundance is necessary but not always sufficient for good recruitment and that other factors, such as habitat and predators, may also be important. Further, work to improve the input parameters and to validate these simulation results is certainly needed. For example, the results are certainly sensitive to the larval depth distribution as a function of larval age. Because these simulations produce near-real time spatial distributions, larval surveys could be designed to sample larvae in areas where the simulations show high and low larval densities in order to evaluate the model results. The model results can also be evaluated by comparing bank-specific recruitment index time series against estimated recruitment to the fishery three years later. Further, genetic studies based on DNA analyses may be more sensitive than the earlier electrophoretic studies in testing the apparent lack of mixing between regions of the archipelago suggested by these simulations. Given the hypothesis that transport was generally from

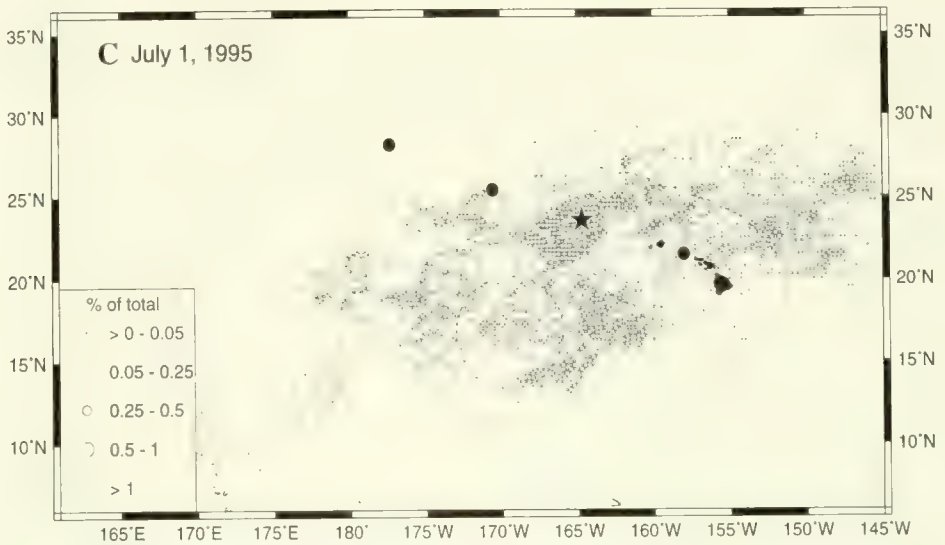


Figure 8 (continued)

Midway to Necker, this results in a testable hypothesis that genetic variance should be greater at Necker than at Midway.

Acknowledgments

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Abstract.—Monte Carlo simulation from probability distributions is often favored as a means of quantifying the uncertainty in the results of a population analysis. Observed data are combined with simulations from a population model by using subjective distributions for model parameters for which no data are available. The results from such methods can unfortunately be inaccurate unless care is taken in the combination of these simulations and the observed data. A Monte Carlo method was proposed at the 1996 meeting of the Scientific Committee of the International Whaling Commission for the assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. We show that this method is potentially inaccurate, and as such, it appears to be unsuited to the bowhead application and thus possibly to other similarly structured management problems.

A proposed stock assessment method and its application to bowhead whales, *Balaena mysticetus*

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The variability in parameter estimates from a population analysis is of great interest to stock assessment scientists. Monte Carlo simulation is an intuitively appealing and easily applied strategy for quantifying this uncertainty. Over the past six years, various Monte Carlo assessment methods for the Bering-Chukchi-Beaufort stock of bowhead whales, *Balaena mysticetus*, have been discussed by the Scientific Committee of the International Whaling Commission (IWC). A Bayesian approach (Raftery et al., 1995) was adopted and used as the basis for the IWC assessment of the stock in 1994. The method was developed after a 1991 Scientific Committee (SC) recommendation that methods for taking full account of uncertainty about inputs and outputs to population dynamics models be developed. An alternative maximum likelihood approach was also used for bowheads (Butterworth and Punt, 1995; Punt and Butterworth, 1996). In contrast to the adopted method, the latter approach does not allow for uncertainty in the values of various biological parameters. Rather, it assumes that they are known exactly.

At the 1996 SC meeting, a modified maximum likelihood assessment to account for uncertainty in biological parameters was considered (Punt and Butterworth, 1997). The assessment method was an application of a Monte Carlo approach developed by Restrepo et al. (1991, 1992). Punt and Butterworth (1997) cited an example of the use of the Monte Carlo approach by the International Commission for the Conservation of Atlantic Tunas, and Restrepo et al. (1992) applied their approach to swordfish and cod fishery assessments.

In our paper, we review the proposed Monte Carlo approach, both in general and in the specific bowhead application, and evaluate its performance and its compliance with established statistical principles. We show that in some circumstances the method can provide suboptimal results for bowhead as-

sessment, and it may thus be unsuitable for more general fisheries management problems. In order to illustrate the potential pitfalls of the method, some simulations were performed. The paper is presented solely as a scientific appraisal of the suggested approach, and the examples given are purely illustrative. We show how modifications of the technique can lead to improved performance, but we do not formally propose any alternative assessment methods here.

The Monte Carlo approach

Description

Restrepo et al. (1992) described an approach to quantifying the uncertainty in the results of sequential population analyses for various fish stocks. They motivated their approach by noting that

> Fisheries managers recognize the dangers of accepting parameter estimates without consideration of the variability inherent in the estimates of fish stock status and related parameters... If all sources of error are not appropriately accounted for, then estimates of the uncertainty in the assessment results may be too small.

This Monte Carlo approach (hereafter MCA) proceeds as follows. Probability distributions are used to describe uncertainty in the inputs to an assessment model. These distributions are constructed in two ways:

1 If observed data are available for a specific input, a parametric statistical model for the data is assumed, and the parameters are estimated by maximum likelihood. A parametric bootstrap is then used to obtain a sample of input values. These values are used as values of the input in the assessment model.
2 If no data relevant to the input are available, a subjective "prior" distribution, representing educated guesses about the true value, is placed upon it.[1] A sample from this prior is used in the assessment model.

The second case occurs in many stock assessment procedures. For instance, a prior was needed for natural mortality, M, in the swordfish assessment of Restrepo et al. (1992). Similarly, we required a subjective distribution for the growth rate parameter, MSYR in the bowhead whale example in the section "Application of MCA to bowhead whale assessment."

[1] Such a distribution is effectively a Bayesian prior distribution. However, since the framework of MCA is not Bayesian, Restrepo et al. (1992) do not refer to such a distribution as a prior.

The next step in MCA is to compare simulated model outputs, such as a time trajectory of stock sizes to observed data, in order to formulate a likelihood (assuming lognormal deviations). Many input parameter sets are drawn randomly from the specified input distributions (i.e. either from data-based bootstrap or subjective prior), and for each set, a conditional maximum likelihood estimate (MLE) is calculated for quantities of interest, given the fixed input parameters and the observed data. The simulation distribution of such conditional MLEs is used to quantify uncertainty. The simulation is viewed as translating input uncertainties into output uncertainties.[2]

MCA is suggested for situations where (possibly many) nuisance parameters exist. These are typically the model input parameters for which no informative data are available. The basic strategy is to estimate the quantities of interest (e.g. current stock size and production rate) conditional on values of the nuisance parameters and then to integrate over the prior for the nuisance parameters. The distribution of the conditional estimates of the parameters of interest is then examined for the purposes of inference. For example, if $\hat{\theta}_\gamma$ is an estimator of θ, conditional on nuisance parameters γ, then

$$\hat{\theta}_{(1)} = \int \hat{\theta}_\gamma p(\gamma) d\gamma \qquad (1)$$

is an MCA estimate of θ, where $p(\gamma)$ is the prior for γ.[3]

In practice, the integral in Equation 1 is not calculated exactly; it is approximated by using the Monte Carlo simulation described above. In the form of an algorithm, MCA proceeds as follows:

1 Obtain the MLE $\hat{\theta}_{\gamma_0}$ from the observed data $\boldsymbol{X}$ and a likely value γ_0.
2 Sample γ^* from the prior $p(\gamma)$.
3 Sample pseudo-data $\boldsymbol{X}^*$ from a distribution with density $f(\boldsymbol{x}; \hat{\psi}(\boldsymbol{X}))$, where $f(\boldsymbol{x}; \psi)$ is a model for the data but not necessarily the assessment model and where $\hat{\psi}(\boldsymbol{X})$ is an estimate of the parameters of this model. $\hat{\psi}(\boldsymbol{X})$ may depend on the results of step 1, namely $\hat{\theta}_{\gamma_0}$ and γ_0, or even on standard MLEs $\hat{\theta}$ and $\hat{\gamma}$. An example of f would be to assume $\boldsymbol{X}^* \sim N(\boldsymbol{X}, \hat{\psi})$, where $\hat{\psi}$ is an estimated dispersion matrix.

[2] Restrepo et al. (1992) also consider uncertainty in the assessment model itself, but this issue is not of primary interest here. In the bowhead whale application, the assessment model is fixed by the IWC.

[3] In general these parameters may be multivariate vectors. For simplicity, we restrict our focus to scalar parameters in the subsequent examples.

4 Find the conditional MLE $\hat{\theta}_{\gamma^*}$ given γ^* by using the simulated data $\boldsymbol{X}^*$. Store this value.
5 Repeat steps 2–4 many times to obtain a collection of $\hat{\theta}_{\gamma^*}$'s.

MCA inference about θ is then based on the distribution of this collection of $\hat{\theta}_{\gamma^*}$'s. Typically, the original $\hat{\theta}_{\gamma_0}$, or the mean or median of the Monte Carlo sample, is used as a point estimate, and the 0.025 and 0.975 quantiles form the bounds of a 95% confidence interval.

The Monte Carlo approach is not a straightforward extension of a sensitivity analysis. Usually, in a sensitivity analysis, a small number of alternative parameter values are tried, and the individual point estimates and confidence intervals obtained by using each parameter set are tabled. Inference usually follows from a single analysis where a particular baseline parameter has been set; the remainder of the table is used to assess how conclusions would change under different modeling assumptions. With MCA, a potentially vast number of parameter values are tried, and an overall confidence interval is obtained by pooling the results of each individual analysis, effectively integrating over the distribution of the nuisance parameters. We show in the rest of this paper that this integration is a source of potential bias.

The MCA technique is potentially highly sensitive to violations of its assumptions. If one is going to express uncertainty in the value of a parameter by means of a probability distribution, then this distribution should be treated as a prior in a fully Bayesian setup. The method given in Equation 1 provides estimators that will not necessarily possess the desirable properties of either Bayesian or ML estimators. A general overview of Bayesian methods is given by Lee (1997).

In a Bayesian framework, the best estimator of θ (with respect to squared error loss) is the posterior mean $E(\theta|\text{data})$, therefore it would be better to define the estimator as

$$\hat{\theta}_{(2)} = E(\theta|\text{data}) = E\big[E(\theta|\gamma,\text{data})\big] = \int \hat{\theta}_\gamma \pi(\gamma|\text{data})\, d\gamma, \quad (2)$$

where $\hat{\theta}_\gamma$ = the posterior mean of θ conditional on γ, and
$\pi(\gamma|\text{data})$ = the posterior distribution of γ.

One might regard Equation 2 as a general strategy and use it in cases where $\hat{\theta}_\gamma$ is not necessarily the Bayesian estimator. In this case, however, the properties of $\hat{\theta}_{(2)}$ are not clear.

A simple point estimation example

Schweder and Hjort[4] first identified potential weaknesses with MCA, and they described two situations where differences between the methods of Equations 1 and 2 arose. The first of these is repeated here: consider a random sample of size n from a normal distribution with mean μ and variance σ^2, denoted $X_i \sim N(\mu, \sigma^2)$ for $i = 1, \ldots, n$. Assume that there is a $N(\mu_0, \tau_0^2)$ prior for μ, where μ_0 and τ_0^2 are the prior mean and variance respectively. Let σ^2 be the parameter for which inference is desired. μ is a nuisance parameter and σ^2 is regarded as fixed. The maximum likelihood estimate of σ^2 conditional on μ is

$$\hat{\sigma}^2_\mu = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu)^2.$$

The estimators given by Equations 1 and 2 are then

$$\hat{\sigma}^2_{(1)} = E_{prior}(\hat{\sigma}^2_\mu) = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu_0)^2 + \tau_0^2$$

and

$$\hat{\sigma}^2_{(2)} = E_{posterior}(\hat{\sigma}^2_\mu) = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu_{post})^2 + \tau^2_{post}$$

respectively, where μ_{post} and τ^2_{post} are the posterior mean and variance of the nuisance parameter μ. For this simple case, we have closed form expressions for Equations 1 and 2, and no Monte Carlo sample from the prior for μ is required. Note that in Equation 2, $\hat{\sigma}^2_\mu$ (the conditional maximum likelihood estimator of σ^2) is used as $\hat{\theta}_\gamma$. In addition we note that $\hat{\sigma}^2_{(2)}$ depends on σ^2 because both μ_{post} and τ^2_{post} are functions of σ^2. In other words, the estimator $\hat{\sigma}^2_{(2)}$ depends on the quantity it is trying to estimate. This occurs when $\hat{\theta}_\gamma$ is not the Bayesian posterior mean of θ conditional on γ. In our examples, we simply plugged in the ordinary MLE where needed to remove this dependency. Thus, to evaluate $\hat{\sigma}^2_{(2)}$ here, $\hat{\sigma}^2_{std}$ was used as a plug-in estimate of σ^2 in the expressions for μ_{post} and τ^2_{post}. $\hat{\sigma}^2_{std}$ is the usual MLE of σ^2 and is what would normally be used if conditioning on μ were not of interest.

We know from standard theory that $\hat{\sigma}^2_{std} \to \sigma^2$ as $n \to \infty$. Because $\tau^2_{post} \to 0$ and $\mu_{post} \to \mu$, we have that $\hat{\sigma}^2_{(2)} \to \sigma^2$ as $n \to \infty$. $\hat{\sigma}^2_{(1)}$, on the other hand, will converge to σ^2 only if $\mu_0 = \mu$ and $\tau_0^2 = 0$. It follows that $\hat{\sigma}^2_{(1)}$ will, in general, yield accurate estimates only if

[4] Schweder, T., and N. L. Hjort. 1997. Indirect and direct likelihoods and their synthesis—with an appendix on minke whale dynamics. Paper SC/49/AS9 presented to the IWC Scientific Committee, October 1997.

μ_0 is close to μ and τ_0^2 is small. We show later the practical implications of choosing an estimator for which the data either do ($\hat{\sigma}^2_{(2)}$) or do not ($\hat{\sigma}^2_{(1)}$) eventually dominate the prior.

An alternative approach that does not involve conditioning on μ is a fully Bayesian analysis where both μ and σ^2 are random variables. This approach requires the specification of a joint prior on μ and σ^2. One such prior is the indifference or "reference" prior (Jeffreys, 1961)

$$p(\mu,\sigma^2) \propto \frac{1}{\sigma^2}.$$

The resulting marginal posterior mean of σ^2 is the best Bayesian estimator of this parameter and is given by

$$\hat{\sigma}^2_{(3)} = \frac{1}{n-3}\sum_{i=1}^{n}(x_i - \bar{x})^2.$$

To investigate the difference between the MCA estimate in Equation 1 and the ad hoc "Bayes" approach in Equation 2, we performed some simple simulations. For each of nine combinations of μ_0 and τ_0^2, a random sample of size n = 1000 was drawn from a $N(\mu=50, \sigma^2=100)$ distribution. In each case, $\hat{\sigma}^2_{(1)}$, $\hat{\sigma}^2_{(2)}$, $\hat{\sigma}^2_{(3)}$, and $\hat{\sigma}^2_{std}$ were determined. The results are shown in Table 1.

The results show very poor performance for $\hat{\sigma}^2_{(1)}$, and good, similar performances for $\hat{\sigma}^2_{(2)}$, $\hat{\sigma}^2_{(3)}$, and $\hat{\sigma}^2_{std}$. In this simple case, the analyst would presumably never choose MCA or the ad hoc "Bayes" method over optimal estimators, such as $\hat{\sigma}^2_{(3)}$ and $\hat{\sigma}^2_{std}$. The key point of this example is that if conditioning on nuisance parameters is to be used, the strategy presented in Equation 2 appears to be preferable to the MCA estimate in Equation 1. As mentioned earlier, the use of Equation 2 has a severe limitation of its own; we therefore do not regard it as a viable alternative approach.

There is considerable literature on the role of conditioning in inference. Reid (1995) has presented a review of recent developments.

Table 1

Simulation results for the example of Schweder and Hjort (See Footnote 4 in the main text).

		Estimators of σ^2 (true value is 100)			
μ_0	τ_0^2	MCA: $\hat{\sigma}^2_{(1)}$	Ad hoc "Bayes": $\hat{\sigma}^2_{(2)}$	Full Bayes: $\hat{\sigma}^2_{(3)}$	Std. MLE: $\hat{\sigma}^2_{std}$
50	1	95.4	94.5	94.7	94.4
	9	102.0	93.0	93.2	92.9
	25	121.0	95.9	96.1	95.8
60	1	198.4	100.4	99.8	99.5
	9	197.2	92.1	92.3	92.0
	25	220.8	99.9	100.1	99.8
70	1	499.8	106.6	103.4	103.1
	9	490.0	106.4	106.5	106.2
	25	530.4	109.7	110.0	109.6

Confidence interval estimation

The example in the section "A simple point estimation example" illustrates poor performance for MCA with regards to point estimation. Similar problems occur when constructing confidence intervals.

Consider the following example: let $X_i \sim U(\gamma-\theta\gamma, \gamma + \theta\gamma)$ for $i = 1,\ldots,100$, denote a random sample from a uniform distribution with bounds specified by the given functions of θ and γ. Let γ be the nuisance parameter. The unconditional MLEs are $\hat{\gamma} = (\max X_i + \min X_i)/2$ and $\hat{\theta} = (\max X_i - \min X_i)/(\max X_i + \min X_i)$. The conditional MLE of θ given γ is $\hat{\theta}_\gamma = (\max X_i - \min X_i)/(2\gamma)$.

Suppose the nuisance parameter, γ, has a $U(a,b)$ prior, $0 \le a < b$. MCA would proceed as follows:

1 Sample $\gamma^* \sim U(a,b)$.
2 Use the parametric bootstrap (e.g. Efron and Gong, 1983) to sample $X_i^* \sim U(\hat{\gamma}-\hat{\theta}\,\hat{\gamma}, \hat{\gamma}+\hat{\theta}\,\hat{\gamma}), i = 1, \ldots, 100$.
3 Find the conditional MLE, $\hat{\theta}_{\gamma^*}$, using the bootstrap data, and conditioning on the current γ^*.
4 Store $\hat{\theta}_{\gamma^*}$ and go to step 1. Use the collection of $\hat{\theta}_{\gamma^*}$'s to obtain a confidence interval with the quantile method.

The ad hoc "Bayes" method, which relies on sampling from the posterior, proceeds with the same steps except that step 1 is replaced by

1. Sample γ^* from its posterior distribution.

Here, if we think of the likelihood as a function of γ only, then the posterior for γ is proportional to

$$\prod_i \left[\frac{1}{2\theta\gamma} I(\gamma-\theta\gamma \le X_i \le \gamma+\theta\gamma)\right] I(a \le \gamma \le b),$$

where I is an indicator function given by

$$I(x) = \begin{cases} 1 \text{ if } x \text{ is True} \\ 0 \text{ if } x \text{ is False.} \end{cases}$$

Because this posterior depends on θ, we plugged in $\hat{\theta}$ in the same way as we did for the ad hoc "Bayes" method in the section "A simple point estimation example."

In a simulation example, we let $\theta = 4$, $\gamma = 4$, $a = 0$, and $b = 8$, so that the true value for γ was at the midpoint of its prior. The MLEs were $\hat{\theta} = 4.06$ and $\hat{\gamma} = 3.88$. The 95% MCA interval for θ was (1.99, 87.55). The interval obtained with the ad hoc "Bayes" method was (3.78, 4.03). The MCA interval was 342 times wider than the second interval, and 2.7 times wider than the range of the observed data.

Note that the MLE $\hat{\theta}$ is not contained in the second interval above. This is an undesirable result of the ad hoc "Bayes" method here. One possible remedy is as follows: instead of simply plugging $\hat{\theta}$ into the posterior for γ each time we sample from it, we could attempt to "integrate over theta" by plugging in a different estimate of θ on each occasion. Each of these plug-in values for θ can be obtained by calculating the MLE of θ from a nonparametric bootstrap sample of the real data X. The confidence interval resulting from this strategy was (3.59, 4.08), so the MLE is now contained in the interval. We stress that this is again an ad hoc solution and we strongly favor standard maximum likelihood or Bayesian methods over either MCA or the ad hoc "Bayes" method.

Finally, the example can also be twisted so that the MCA interval is too narrow. Suppose $X_i \sim U(\gamma - \theta\gamma^2, \gamma + \theta\gamma^2)$. This leads to $\hat{\theta}_\gamma = (\max X_i - \min X_i)/(2\gamma^2)$, a cusp-shaped function of γ over any interval that includes 0. Thus, considering γ priors of the form $U(-a,a)$ for $a > 0$, we observed that MCA leads to the surprising result that the width of a quantile-based confidence interval for θ approaches 0 as a increases, while holding the observed data fixed. In other words, the width of the confidence interval is entirely dependent on the prior, and wider priors lead to narrower MCA confidence intervals.

Application of MCA to bowhead whale assessment

Punt and Butterworth (1997) examined the applicability of MCA in the assessment of the Bering-Chukchi-Beaufort stock of bowhead whales. As with the swordfish assessment of Restrepo et al. (1992), the approach involved generation of pseudodata with a parametric bootstrap. In the bowhead case, the real data consisted of abundance estimates and corresponding CV estimates for several years, and observed age-class proportions. Thus, each MCA simulation consisted of the following:

1 *Bootstrapping of data.* A series of pseudo-abundance estimates is bootstrapped from the observed data (Table 1 in Punt and Butterworth, 1997). Each estimate is assumed to be independent and from a lognormal distribution with mean and CV equal to the observed estimates from that year. Pseudodata for fractions of calves and matures are generated from Table 4 of IWC (1995).
2 *Sampling of biological nuisance parameters from priors.* Parameters such as age at maturity and natural mortality rates are generated from prior distributions from IWC (1995).
3 *Conditional estimation.* Conditional on the values of the nuisance parameters, maximum likelihood estimation is used with an age-structured density dependent population dynamics model to obtain estimates of the parameters of interest: carrying capacity (K) and a productivity parameter (MSYR). The likelihood contains contributions from both the abundance and proportion data.
4 *Uncertainty estimation.* The variation in conditional MLEs is used to represent uncertainty.

Note that K and MSYR are the parameters of interest (denoted by θ in our previous notation), whereas the other biological parameters take the role of γ. The distributions from which they were simulated are the prior distributions. The results of 1000 replications of this procedure are used to form confidence intervals.

A simple population dynamics model

For the purposes of illustration, we applied MCA to a simple population dynamics model (PDM). This is a non-age-structured density dependent PDM given by

$$P_{t+1} = P_t - C_t + 1.5(MSYR)P_t\left(1-(P_t/K)^2\right), \quad (3)$$

where P_t = the population in year t, with $t = 0$ corresponding to the baseline year before commercial hunting started (here 1848);
K (or P_0) = the initial population size or carrying capacity;
MSYR = the maximum sustainable yield rate of production as a proportion of the population aged 1+; and
C_t = the number of whales killed by hunting in year t (known exactly).

This model is much simpler than the BALEEN II PDM (de la Mare and Cooke[5]) used by the IWC for

[5] de la Mare, W. K., and J. G. Cooke. 1993. "BALEEN II: The population model used in the Hitter-Fitter Programs". Unpublished manuscript available from the IWC Secretariat, The Red House, 135 Station Road, Histon, Cambridge, UK CB4 4NP.

bowhead assessment, but it nevertheless captures many of the essential features of the bowhead population. The model is viewed as having two inputs (K and MSYR) and one output (P_{1993}); with fixed values of MSYR and the initial K, Equation 3 is applied recursively until P_{1993} is obtained. We use the term "model input" for input parameters whose true value is uncertain. Since the time series of catches C_t is exactly known, we regard it as a set of constants in Equation 3, rather than as a set of model inputs.

In our simplified version of the bowhead analysis, we treated MSYR as a nuisance parameter (γ in our previous notation) and K was the parameter of interest (the θ from before). The only parameter about which we observed data for a parametric bootstrap was P_{1993}. MSYR was assigned a subjective prior distribution. In terms of implementation, we ran the model "backwards" with P_{1993} and MSYR as inputs and K as output. A Newton-Raphson algorithm was used to solve for K. As a result, we effectively had P_{1993} and MSYR as model inputs, and K (obtained conditionally on MSYR and the data) as the model output.

Implementation of MCA and a Bayesian approach

To evaluate MCA, we examined its performance when the true whale stock status was known. "True" values of K and MSYR were selected, and the PDM was run to obtain the "true" value of P_{1993}. Because K (the parameter of interest here) has a "true" value, we were able to assess the accuracy of the estimates produced by the simulations.

MCA was applied to the simple PDM of Equation 3 in a number of steps. The prior for the nuisance parameter MSYR was gamma(8.2, 372.7), and the likelihood for the observed total population in 1993 was $N(P_{1993},626^2)$. These choices were based on IWC consensus (IWC, 1995) and were the same as used in previous work (Raftery et al.[6]).

We assumed that we had a single observation from the likelihood for P_{1993}. In practice such an observation is usually obtained by means of a census. The observation is typically a maximum likelihood estimate of P_{1993}, therefore we denoted it by $\hat{P}_{1993}$.

An original conditional MLE was obtained by conditioning on a "likely" point estimate of MSYR, say $MSYR_0$. We chose $MSYR_0 = 0.02$, the mean of the prior for MSYR. The model was then run backwards (i.e. with $\hat{P}_{1993}$ and $MSYR_0$ as inputs) and the likelihood maximized. The resulting output was the conditional maximum likelihood estimate $\hat{K}_{MSYR_0}$ of K because (given $MSYR_0$) it lead to the value of P_{1993} that maximizes the likelihood.

The MCA estimation then proceeds as follows:

1 Draw $\hat{P}^*_{1993}$ from $N(\hat{P}_{1993},626^2)$. This is the parametric bootstrap from a distribution with mean given by the observed total population in 1993.
2 Draw $MSYR^*$ from the prior for MSYR.
3 Obtain $\hat{K}_{MSYR^*}$ by running the model backwards with $\hat{P}^*_{1993}$ and $MSYR^*$ as inputs.
4 Repeat steps 1–3 many times to form a collection of $\hat{K}_{MSYR^*}$ estimates. Like Punt and Butterworth (1997), we used 1000 replications.
5 Use $\hat{K}_{MSYR_0}$ and the distribution of the $\hat{K}_{MSYR^*}$ estimates to obtain inference about K. Specifically, the distribution of the $\hat{K}_{MSYR^*}$ estimates shows how the conditional MLE of K changes as MSYR is varied according to its prior.

For comparison with MCA, consider a fully Bayesian analysis which involves specifying priors for every model parameter, i.e. K, MSYR, and P_{1993}. This introduces an extra complication in that the input distributions and the model together induce a distribution on the output. There are thus two distributions (the specified prior and the induced distribution) on the output that need to be combined or reconciled in some manner. For our "backwards" implementation of the model here, the priors for MSYR and P_{1993} induce a prior on the output K. This issue has received considerable attention at the IWC and work in the area is ongoing. A possible solution involving logarithmic pooling of the two distributions is discussed in Raftery et al.[6] and Raftery and Poole.[7]

For this example, it was useful to compare a Bayesian approach with MCA, but avoiding the added complexity of the prior incoherence. This could be achieved if we simplified the Bayesian analysis slightly by ignoring the prior on the output K. We had a prior for MSYR and a likelihood for P_{1993} as we did in the MCA implementation above. In addition, we now also had a $N(7800,1300^2)$ prior for P_{1993}. This was the prior used in Raftery et al.[6] and was again based on IWC consensus. The prior and likelihood were combined to yield a posterior distribution for P_{1993}. Because we had no data on MSYR, its prior was not updated to a posterior. The only operational difference between MCA and the Bayesian method was in the generation of values for P_{1993}: with MCA,

[6] Raftery, A. E., D. Poole, and G. H. Givens. 1996. The Bayesian synthesis assessment method: resolving the Borel Paradox and comparing the backwards and forwards variants. Paper SC/48/AS16 presented to the IWC Scientific Committee, June 1996.

[7] Raftery, A. E., and D. Poole. 1997. Bayesian synthesis methodology for bowhead whales. Paper SC/49/AS5 presented to the IWC Scientific Committee, October 1997.

values were bootstrapped from a distribution whose parameters were determined by maximum likelihood; with Bayes, they were sampled from the posterior.

Simulation results

Simulations were performed by using three sets of "true" parameters as shown in the first three columns of Table 2. The values of MSYR in these three sets of simulations correspond to the 0.5, 0.975, and 0.025 quantiles (respectively) of the gamma (8.2, 372.7) prior for this parameter. In this way, we investigated the performance of the method when the true MSYR is at the center and the boundaries of its prior 95% probability interval. In each case, a value of K was chosen such that extinction did not occur and P_{1993} was positive.

The first set of simulations represents a scenario where the mean of the prior for MSYR happens to coincide with the true value. If we use the prior mean as a point estimate (or "best guess") of MSYR, then our point estimate and the true value are the same. For this set, then, we would expect all assessment methods to provide accurate inference about K. The remaining two sets of simulations represent scenarios where our prior is inaccurate, i.e. the true MSYR is either larger or smaller than the prior mean (which remains unchanged). In these cases, this inaccuracy is naturally going to cause the resulting distribution of the output K to be biased. All assessment approaches will be affected by this bias, particularly with respect to their point estimates of K. Indeed, these parameter sets represent situations that all assessment scientists would like to avoid. The key point of interest is the extent to which a method can be insensitive to poor prior information and still provide somewhat reliable inference.

The results of the simulations are shown in Table 2. For each of the three sets of true parameters, the MCA analysis was run three times by using the 0.025, 0.5, and 0.975 quantiles of the normal likelihood as the observed 1993 population, $\hat{P}_{1993}$. Then, this entire simulation design was replicated 500 times. The quantiles shown are MCA medians for $\hat{K}_{MSYR^*}$ across the 500 replicates, and the coverage rates (last two columns) show the percentage of the 500 replicates for which the estimated 95% MCA or Bayes confidence interval covered the truth.

In the first set of simulations, where the true MSYR and the prior mean MSYR_0 were exactly equal, the conditional MLE $\hat{K}_{MSYR_0}$ was very accurate. This is to be expected in this optimistic (if somewhat unlikely) scenario. The MCA confidence intervals provided by $\hat{K}_{MSYR^*}$ covered the true K in all cases, as did the confidence intervals obtained with the Bayesian method. Also, the estimation was fairly insensitive to the accuracy of the estimate $\hat{P}_{1993}$. A difference of 1227 whales in the estimate of P_{1993} (i.e. two standard deviations) resulted in $\hat{K}_{MSYR0}$ changing by less than 100 whales.

In the second set, the true value of MSYR was greater than the prior mean. This resulted in K having been overestimated. Here, both MCA and Bayesian results were biased by the use of the same bad prior, but the MCA coverage was worse. If follows that the suboptimal behavior of MCA cannot be attributed solely to the choice of prior. The 95% MCA intervals provided poor coverage of the truth, worse when $\hat{P}_{1993}$ was accurate than when it was too low. For the Bayesian method, this difference was not as great. The coverage of the Bayesian intervals was somewhat better in two cases, particularly when $\hat{P}_{1993}$ was too large.

In the final set, the true value of MSYR was at the low end of the prior interval, and we observed that K

Table 2

Simulation results for the simple bowhead whale population dynamics model (PDM).

Parameter set					MCA quantiles, $\hat{K}_{MSYR}$			Coverages	
MSYR	K	P_{1993}	$\hat{P}_{1993}$	$\hat{K}_{MSYR_0}$	0.025	0.5	0.975	MCA (%)	Bayesian (%)
0.02	14,700	8,733	7,506	14,640	11,230	14,360	18,870	100	100
			8,733	14,700	11,260	14,400	19,160	100	100
			9,960	14,780	11,330	14,450	19,540	100	100
0.04	11,300	9,896	8,669	14,700	11,250	14,400	19,120	68	66
			9,896	14,780	11,290	14,470	19,450	55	63
			11,123	14,880	11,580	14,560	19,840	0	23
0.01	18,500	6,971	5,744	14,570	11,270	14,300	18,430	38	54
			6,971	14,620	11,260	14,340	18,710	80	88
			8,198	14,670	11,270	14,380	19,000	99	99

was underestimated by about 4000 whales for all three values of $\hat{P}_{1993}$. The estimates of K were inaccurate regardless of the accuracy of $\hat{P}_{1993}$. Although not shown, this inaccuracy holds for the Bayesian method as well as for MCA. Both methods provided the best coverage when $\hat{P}_{1993}$ was too large, but the Bayesian method provided better coverage than MCA in the other two cases. Again, these results separated coverage problems attributable to inaccurate priors from additional performance degradation apparently introduced by opting for MCA analysis.

As a final point, these simulations and others that we ran suggest that the MCA estimates of K are heavily dependent on the prior distribution for MSYR, to the point of being undesirably insensitive to the true values of K, P_{1993}, and the data $\hat{P}_{1993}$. This behavior is more extreme than would be the case if the prior was updated to a posterior in a fully Bayesian framework. These results concur with the results in the section "A simple point estimation example," where the MCA estimates were greatly influenced by the prior mean and variance. When the prior is accurate and precise, MCA may perform well, as will Bayesian techniques. Bayesian techniques seem to weight the data more heavily in relation to the prior, than does MCA.

Relation between MCA and bootstrap

The MCA approach described in the section "Implementation of MCA and a Bayesian approach" included bootstrapping the abundance data unconditionally. A standard (conditional) bootstrap would proceed by resampling the residuals (e.g. Efron and Gong, 1983, p. 43) from the model fit. The unconditional approach used in the bowhead application introduced excess variability because bootstrapped pseudodata varied about the observed data, which in turn varied about the model fit.

The general MCA approach might be viewed as an approximation to a bootstrap that is unconditional on the model fit. In such applications (e.g. Smith and Gavaris, 1993), the interpretation of the stochasticity thereby introduced must be carefully considered if it differs from the data stochasticity that causes estimation uncertainty. When, as is permitted with MCA, the unconditional approach simulates from a subjective prior rather than from data, the method is not a bootstrap because the simulation reflects stochasticity other than that introduced by data used for estimating the parameter.

Even in the case when sufficient data are available to permit parametric bootstrap simulation of all inputs (case 1 in the section "The Monte Carlo approach"), MCA does not reduce to a parametric bootstrap of the desired estimator. A parametric bootstrap expresses sampling uncertainty about a statistic $R(\boldsymbol{X}, F(\theta))$, where $\boldsymbol{X} \sim F$, by observing the distribution of $R(\boldsymbol{X}^*, \hat{F}(\theta))$, where $\hat{F}$ is an estimate of F that depends on the data $\boldsymbol{X}$, and $\boldsymbol{X}^* \sim \hat{F}$. Variability in R is due to $\boldsymbol{X}$. A parametric bootstrap arises when a model $\hat{F}(\theta) = F(\theta)$ is fitted, or less desirably $\hat{F}(\theta) = G(\hat{\gamma})$ in some applications of MCA. In this case, $\hat{\theta}$ or $\hat{\gamma}$ should be estimated from the data, $\boldsymbol{X}$, whose stochasticity induces sampling variability in $R(\boldsymbol{X}, F(\theta))$. However, with MCA, $\hat{\theta}$ or $\hat{\gamma}$ is estimated from different data, not the data on model output parameters, although it is the uncertainty associated with estimators of output parameters that is desired. Even in this case, the sampling distributions used are effectively data-based priors, and MCA relies on the unusual approach of integrating a conditional maximization of the likelihood over the prior.

Conclusion

Theoretical investigation and simulation show that the combination of Bayesian and conditional maximum likelihood techniques used by MCA has the potential to yield quite variable or biased results, or both, though it can perform well in ideal circumstances. In some situations, a fully Bayesian or classical ML solution can be obtained by small modifications to MCA, and the optimal properties of these more standard methods are well known. For more complex problems, Bayesian and ML solutions are sometimes more difficult to obtain than is an MCA solution. However, as our examples illustrate, MCA can result in unreliable inference even in simple situations. MCA integrates a conditional maximization of the likelihood over the prior, whereas a fully Bayesian approach integrates a conditional mean. If one uses what is effectively a Bayesian prior, then it is suboptimal to use it in a non-Bayesian inference framework.

We have seen how MCA produces estimates with excessive bias. However, there may exist classes of assessment problems where, owing to some feature that is identifiable in advance, the extra bias is acceptably small. MCA could be applied to such problems because the excess bias would not cause MCA results to differ much from results produced by either fully Bayesian or ML methods. Our bowhead whale and simple examples clearly do not belong to such a class. Furthermore, in the general case, the extent to which MCA might err is not controllable or estimable by the analyst. Although MCA can produce good estimates in some applications, a method that can also go badly wrong is risky when one does not

know the extent of problems in any particular application. When priors are used, the usefulness of Bayesian approaches (when obtainable) would seem to be greater than MCA, because the effect of the priors is washed out with increasing data (contrary to what happens with MCA). When priors are not required, either Bayesian or MLE techniques might be usefully applied.

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Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa

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Abstract.—Ages of white sharks, *Carcharodon carcharias*, from the east coast of South Africa were estimated by counting growth rings (GRs) in vertebral centra and relating them to length and mass. The vertebrae of 61 females (128–297 cm precaudal length (PCL)) and 53 males (142–373 cm PCL) were examined. Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). X-radiography was used to enhance the visibility of the GRs in whole centra. Counts were made directly from the x-radiographs by one reader and from scanned x-radiographs by two readers. Count precision for each method and reader was determined by using the average percentage error (APE) index which ranged from 5.3 to 6.1%.

One shark injected with oxytetracycline (OTC) was recaptured after 942 days at liberty. The shark was tagged at 140 cm and 46 kg and grew 69 cm and 104 kg. The OTC was visible in the vertebra and there was evidence of annual growth ring deposition. This could, however, not be confirmed with centrum analyses of the entire sample.

The number of GRs counted varied in the following manner. The female and male with the lowest number of GRs, had 0 GR (131 cm PCL) and 1 GR (142 cm PCL), respectively. The female and male with the highest number of GRs, had 8 GRs (282 cm PCL) and 13 GRs (373 cm PCL), respectively. The smallest mature male had 8 GRs (293 cm PCL); there were no mature females. Von Bertalanffy parameters for the combined sexes were L_∞ = 544 cm PCL, k = 0.065/yr, t_0 = –4.4 yr. Growth calculated from predicted lengths decreased from 26 cm for sharks with 1 GR to 12 cm for sharks with 13 GRs. Gompertz parameters were w_0 = 54 kg, G = 3.94, g = 0.094/yr. Growth calculated from predicted mass increased from 23 kg (1 GR) to 94 kg (13 GRs). Back-calculated lengths and mass were lower than observed values and Lee's phenomenon was evident in both back-calculated lengths and mass but not consistently.

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The white shark, *Carcharodon carcharias*, is found worldwide in cold and temperate coastal and shelf waters (Compagno, 1984). As a large, uncommon apex predator, it has received considerable attention from scientists over the past few years. Because of its great resale value, compared with most other sharks, catches of white sharks have increased in various parts of the world, mainly in Australia and South Africa (Compagno, 1990, 1991). Claims of a declining population size in South Australian waters (Compagno, 1991; Bruce, 1992) influenced an initiative to implement protective legislation for this species in South Africa. In 1991 the South African government prohibited the catching or killing of white shark without a permit (Compagno, 1991). This measure was a preemptive protection and is to be reviewed as results of more research into the biology of this species become available (Compagno, 1991). Protection has now also been introduced in California, Florida, and Tasmania (Fergusson et al., in press), as well as in Queensland, New South Wales, South Australia, and Western Australia (Stevens[1])

Legislation in South Africa has prevented this species from being targeted by commercial and recreational anglers. White sharks continue to be caught on the east coast in the nets of the Natal Sharks Board (NSB), which operates a shark control program to protect beach users against shark attack (Cliff et al., 1988). Between 1984 and 1995 an annual average of 40 *C. carcharias* were caught in NSB nets, and 15% were released alive. This activity has formed the basis of a small-scale tagging program that has provided the first estimates of the size of the white shark population (Cliff et al., 1996b). Information about the distribution, diet, movements, and catches of *C. carcharias* in South Africa is available from Bass et al. (1975) and Cliff et al. (1989, 1996a).

Little is known about age and growth of *C. carcharias*, mainly because so few are caught at any one locality, thus hampering collection of vertebral samples for ageing purposes. Knowledge of age at maturity, maximum ages, and growth rates is a prerequisite for age-based methods of stock assessment, which in turn can be used for the management of this species. The only previous attempt at ageing the white shark was that of Cailliet et al. (1985) who had access to only 21 samples, mainly from California. This study attempts to provide age estimates for *C. carcharias* from South Africa from vertebral growth ring counts of 114 sharks.

[1] Stevens, J. D. 1997. CSIRO Marine Laboratories, Tasmania, Australia. Personal comm

Materials and methods

Sampling

Sharks were sampled in NSB nets from 1984 to 1995. Each net was 214 m long, 6 m deep, had a 50-cm stretched mesh, and was set in water 10–14 m deep, parallel to and 300–400 m from shore. For additional details of the netting operation see Cliff et al. (1988).

Precaudal length (PCL) was measured in a straight line from the snout tip to the precaudal notch and is used throughout this study, unless indicated otherwise. To compare our findings with those reported in the literature, the following equations were used to convert lengths:

$$Total\ length\ (TL) = 1.251\ PCL + 5.207$$

(n =36; range 131–307 cm PCL; 95% confidence limits on slope: 1.233 and 1.268; r^2=0.9984) (Cliff et al., 1996a); and

$$PCL = 0.8550\ TL - 0.0955$$

(n =58; range 96–447 cm PCL; 95% confidence limits on intercept: –0.130 and –0.061; r^2=0.996) (Mollet and Cailliet, 1996).

Lengths were converted by means of the method considered most appropriate.

Mass was determined by weighing each shark and subtracting the mass of gut contents where they exceeded 1 kg. Maturity was assessed by the criteria of Bass et al. (1973), where males were considered mature only if their claspers were fully calcified. In females, maturity was based on the presence of distinct ova in the ovary and uteri, which had expanded from a thin, tubelike condition to form loose sacs (Bass et al., 1973; Cliff et al., 1988). Vertebral samples were taken anterior to the origin of the first dorsal fin from 61 females (128–297 cm) and 53 males (142–373 cm). Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). Vertebrae were stored frozen (60%) or in 70% isopropyl alcohol (31%), or dried (9%). Individual centra were cleaned by removing the connective tissue from the corpus calcareum with forceps. Dried samples needed additional soaking in a 5% solution of sodium hypochlorite for 20–40 minutes.

Ring counts

X-radiography was used to enhance the visibility of the growth rings. X-radiographs of whole centra were prepared on an Odel Pollux 700 generator with a Comet tube by using Agfa Ortho (Extremity) film and were processed with an Agfa Curix 160 processor. We x-rayed, using mostly oblique exposure, all centra with the corpus calcareum (Figs. 1A and 2A) facing the tube at a set distance of 100 cm. At 50 mA, exposure times ranged from 0.3 to 0.8 seconds and voltage from 28 to 34 kV. The x-radiographs were then scanned with an Agfa Arcus II scanner and Adobe photoshop software. Ulead ImagePals 2 GO! (Ulead Systems, 1992–94) and CorelDRAW! (Corel Corp., 1993) were used to enhance and work with the images.

A growth ring (GR) was defined as a band pair, composed of one calcified (opaque) and one less-calcified (translucent) band (Fig. 1A). The finer, narrower rings (circuli), also observed by Cailliet et al. (1985), were not used for ageing purposes. The angle change on the centrum face (Fig. 2A), a result of the difference between fast intrauterine and slower postnatal growth (Walter and Ebert, 1991), was regarded as the birth mark.

Counts were made directly from the x-radiographs (XRs) by one reader (A) and from the scanned images (SCs) by two readers (A and B). These three ways of viewing the vertebrae will be called methods XR-A, SC-A, and SC-B, for brevity. Each reader made three nonconsecutive GR counts, without knowledge of the shark's length and previous counts. Count reproducibility was determined by using the following four methods:

1 The average percentage error (APE) as described by Beamish and Fournier (1981) in which an upper limit in the APE was arbitrarily set at 20% for each vertebra (samples were discarded if, after a recount, they were still above this limit) and a final APE index was recalculated and an intrareader comparison (XR-A vs. SC-A) and interreader comparison (SC-A vs. SC-B) of APE values were then conducted;
2 The index of precision D (Chang, 1982);
3 The percentage agreement among the three counts for each method; and
4 The percentage agreement in paired GR counts between the methods.

Centrum analyses

Dorsal centrum diameter and dorsal "birth diameter" were measured in a transverse plane along a straight line through the focus of each vertebra (Fig. 2B). The dorsal "birth diameter" was marked on the x-radiographs and screen images. Distance from the focus to the outer edge of each GR (Fig. 2B) was measured on the scanned images by using CorelDRAW!

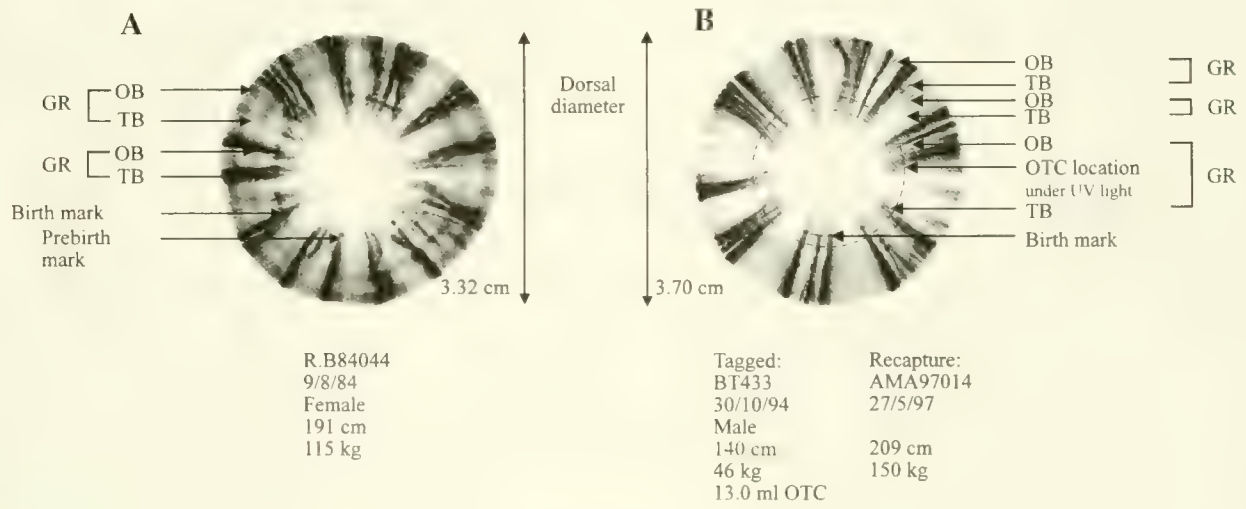

Figure 1

Inverted scanned images of x-radiographs of two white sharks. OB = opaque band, TB = translucent band, GR = growth ring.

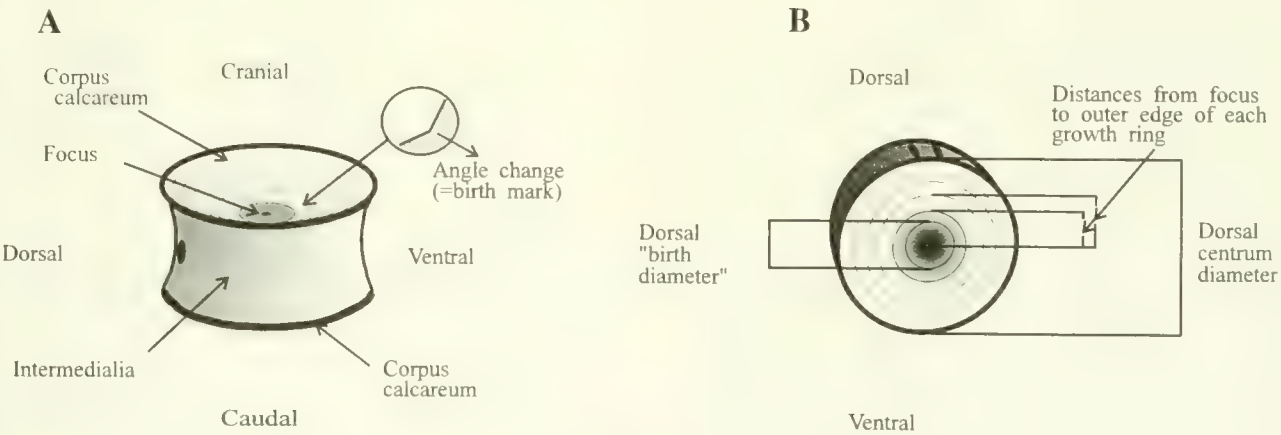

Figure 2

Schematic drawings of a vertebra illustrating terms used in the text.

The relationships between centrum diameter and both shark length and mass were examined by comparing regression lines of both sexes with the procedure of Zar (1974), which compares the slopes and elevations with Student's *t*-tests. Significance levels given in the text are the results of these tests. Outliers were determined by using Statgraphics (STSC, 1991) and eliminated.

The Dahl-Lea method of back-calculation (Carlander, 1969) was used, in which

$$PCL_t = CD_t\,(PCL_c/CD_c),$$

where PCL_t = length at GR t;
CD_t = centrum diameter at GR t;
PCL_c = length at capture; and
CD_c = centrum diameter at capture.

The Monastyrsky method of back-calculation (Bagenal and Tesch, 1978, cited by Francis, 1990) was used to estimate mass at age, in which

$$M_t = (CD_t/CD_c)^b\, M_c,$$

where M_t = mass at GR t;

M_c = mass at capture; and
b = the constant derived from the multiplicative regression of M on CD.

The constant b was derived by using the "body-proportional-hypothesis," where "if a fish at time of capture was 10 per cent smaller than the average fish with the same size of scale, the fish would be 10 per cent smaller than the expected length for the size of that scale throughout life" (Whitney and Carlander, 1956, cited by Francis, 1990).

Confirmation of the annual periodicity of GRs (Cailliet et al., 1983a, 1983b) was attempted with two methods of centrum analyses. First, the last deposited band was classified as translucent or opaque and related to the month of capture (Kusher et al., 1992). The observed and expected ratios of translucent to opaque last bands were then compared. Second, the marginal increment ratio (MIR) (Hayashi, 1976; Skomal, 1990) was calculated with the following equation:

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR = vertebral radius;
R_n = radius to the last complete GR; and
R_{n-1} = radius to the previously completed GR.

Mean MIR, with range and standard error, was then plotted against month.

In addition, 16 white sharks (between 1993 and 1995) were injected with oxytetracycline (OTC) solution (Engemycin, Intervet International B.V.), at a dose of 25 mg per kg body mass as recommended by Holden and Vince (1973) and McFarlane and Beamish (1987). Mass was estimated from the mass-length equation of Cliff et al. (1989). The OTC was administered in several places in the muscle around the first dorsal fin with a 15G × 1.5" disposable needle and 20-mL plastic syringe. Each shark was tagged with an orange identification tag (Hallprint PDA large plastic dart tag), labelled "tetracycline" and given a unique "BT" number.

Age and growth

The program PC-YIELD II (Punt and Hughes, 1989) was used to determine which of 10 different growth models provided the best fit to the data sets obtained by the three methods. Where appropriate, von Bertalanffy growth parameters (VBGP) were computed. The equation (von Bertalanffy, 1938) is

$$L_t = L_\infty (1 - e^{-k(t - t_0)}),$$

Table 1

Comparison of average percentage error (APE) indices and index of precision (D) for each method. Values are given before and after elimination of vertebrae with an APE > 0.2.

Methods	Preliminary APE index (%)	D (%)	n	Final APE index (%)	D (%)	n
SC-A	8.9	6.9	114	5.3	4.1	112
SC-B	12.9	9.8	114	5.4	4.1	108
XR-A	9.0	7.0	114	6.1	3.9	110

where L_t = length at GR t;
L_∞ = maximum theoretical length;
k = the rate at which L_∞ is reached; and
t_0 = the theoretical number of GR at length zero.

To determine whether GR deposition was related to an increase in mass rather than to time of year, Gompertz growth parameters were also calculated. The Gompertz equation (Silliman, 1967; Ricker, 1975) is

$$W_t = w_0 e^{G(1 - e^{-gt})},$$

where w_t = mass at GR t;
G = initial exponential growth; and
g = exponential rate of decline.

Both growth equations were fitted by using the nonlinear regression procedure of STATGRAPHICS, which uses Marquardt's algorithm (Draper and Smith, 1981). Because this procedure is highly dependent upon initial estimates for the parameters, a wide range of initial parameters was used to prevent the models converging to a local minimum, i.e. converging to an unwanted stationary point of the sum of squares, rather than to a global minimum (Draper and Smith, 1981).

Results

Of the 114 processed vertebrae, between two and six, depending on the method, had an APE of over 20% after a recount and were discarded (Table 1). The final APE indices and D values showed little differences amongst methods, indicating similar reproducibility (Table 1). The percentage agreement among the three counts was high, e.g. with method SC-A, for 58.0% of the sample the three counts were the same (Table 2). In all three methods the majority of the readings was the same or differed only by one GR. For this reason, a mean of the three counts was

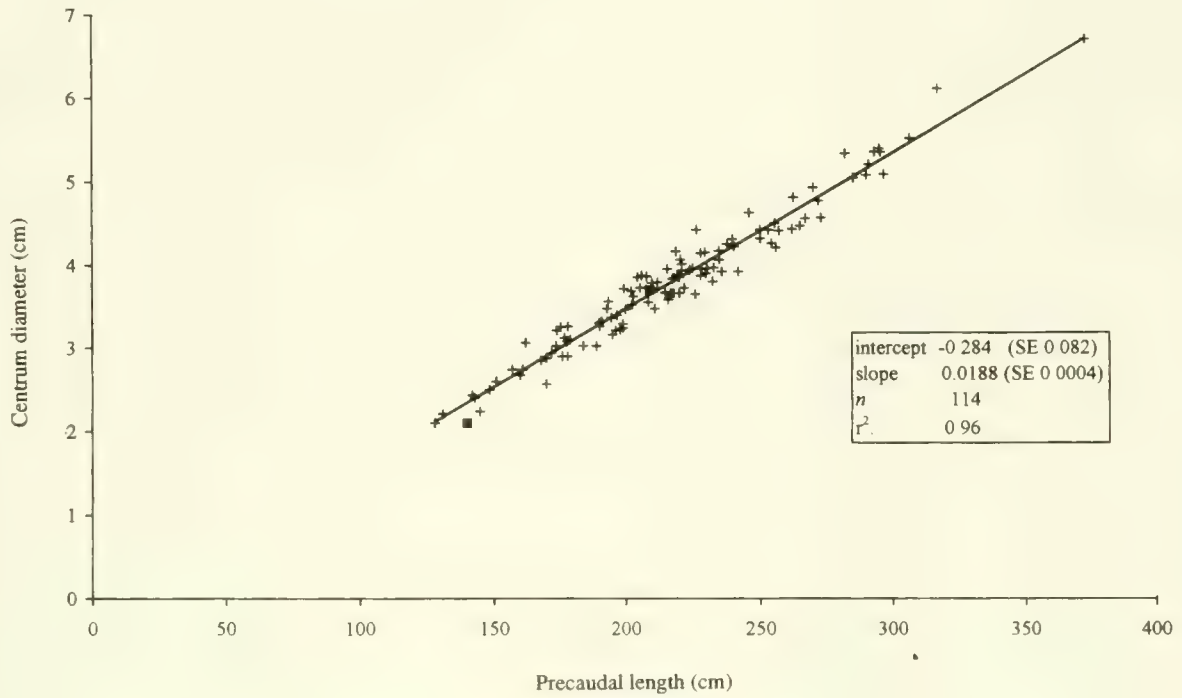

Figure 3

Relationship between centrum diameter and length for combined sexes of the white shark, *C. carcharias*. Squares indicate shark BT433 at tagging and recapture.

Table 2

Percentage agreement among the three counts for each method. Numbers in parentheses indicate sample sizes.

	Difference in GR counts					
Methods	0 GR	1 GR	2 GR	3 GR	4 GR	*n*
SC-A	58.0 (65)	33.0 (37)	7.1 (8)	0.9 (1)	0.9 (1)	112
SC-B	61.1 (66)	37.0 (40)	0.9 (1)	0.9 (1)	—	108
XR-A	50.0 (55)	36.4 (40)	11.8 (13)	1.8 (2)	—	110

Table 3

Percentage agreement in paired growth ring (GR) counts between methods. Numbers in parentheses indicate sample sizes.

	Difference between counts				
Methods	0 GR	1 GR	2 GR	3 GR	*n*
SC-A - SC-B	42.5 (45)	41.5 (44)	15.1(16)	0.9 (1)	106
SC-A - XR-A	59.6 (65)	34.9 (38)	4.6 (5)	0.9 (1)	109

taken as a GR estimate in all three methods and used for all further calculations. The two readers agreed on the mean GR estimate in 42.5% of the vertebrae; in 59.6% of the vertebrae there was no difference between GR estimates obtained by the same reader using the two methods (Table 3).

Centrum analyses

Prebirth marks were found in all vertebrae with method XR-A and in 33% of the vertebrae with method SC-A (Table 4). Using all three methods, we

Table 4

Percentage of vertebrae where prebirth marks were present and nature of the first band after the angle change.

	Prebirth marks		First band after angle change		
			opaque	translucent	
Method	%	*n*	%	%	*n*
SC-A	33	114	94	6	62
SC-B	—	—	96	4	97
XR-A	100	114	88	12	81

Table 5

Observed and back-calculated precaudal length (PCL) at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed PCL (cm)					Back-calculated PCL (cm)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	131	131	131	—	1	85	118	100	7	114
1	128	178	156	16	12	96	182	133	17	112
2	161	228	192	19	18	121	221	165	22	99
3	172	236	204	17	25	150	241	191	24	77
4	197	265	225	16	26	169	270	212	25	46
5	215	291	246	22	15	184	261	222	21	22
6	238	297	276	21	7	212	271	240	18	13
7	263	307	287	19	4	233	294	264	19	10
8	282	293	288	8	2	259	301	279	18	5
9	—	—	—	—	—	278	308	289	16	3
10	317	317	317	—	1	300	335	317	24	2
11	—	—	—	—	—	325	325	325	—	1
12	—	—	—	—	—	338	338	338	—	1
13	373	373	373	—	1	350	350	350	—	1
14	—	—	—	—	—	369	369	369	—	1

found that the majority of the vertebrae had an opaque band as the first band after the angle change (Table 4). Only samples where the nature of the first band was the same in all three counts were considered for our analysis.

A statistically significant linear relation was found between centrum diameter and PCL (Fig. 3). There was no significant difference between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$). Because the intercepts differed only by 0.02, no visual difference in the predicted values of females and males was perceptible, and the common intercept was used to plot a regression for the combined sexes. The intercept was close to zero; therefore no correction, such as the Fraser-Lee method (Carlander, 1969; Branstetter, 1987), was used.

One of the 16 white sharks injected with OTC (BT433) was recaptured after the completion of the study. The shark was tagged during a fishing competition on 30 October 1994; it measured 140 cm and weighed 46 kg. On recapture 942 days later, on 28 May 1997, it measured 209 cm (150 kg). The squares in Figure 3 indicate the length and centrum diameter of this shark at tagging, i.e. at the OTC marker and at recapture.

Because of the similarity of the above regressions for females and males, back-calculations were performed on combined sex data. Mean back-calculated lengths were lower than observed values (Table 5). Lee's phenomenon, a tendency for back-calculated lengths of older fish in the earlier years of life to be systematically lower than those of younger fish at the same age (Carlander, 1969; Smith, 1983), was evident, but not consistent. In sharks with 7 and 8 GRs, for example, the back-calculated values for each GR class were higher than those for sharks with 6 GRs.

A multiplicative relationship was found between centrum diameter and mass and no significant difference was found between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$) (Fig. 4). Again, because of the similarity of the regressions for females and males, back-calculations were performed on combined sex data. Back-calculated mass was lower than observed values (Table 6). Lee's phenomenon was evident, but not consistent, and showed a similar trend to that of back-calculated lengths. Because of the use of mean GRs, the number of observed lengths (or masses) per GR class, plus the number of back-calculated lengths (or masses) in the next GR class, did not always add up to the total number of back-calculated lengths (or masses) of the previous GR class (Tables 5 and 6).

The observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=33$), irrespective of whether opaque band deposition was assumed to occur in summer or in winter. For this analysis only vertebrae were used where the nature of the last band was the same in all nine counts (i.e. in all three counts of all three methods). The exclusion of borderline cases, i.e. only summer months (22 Dec–20 Mar) and winter months (21 Jun–22 Sep), did not alter the result

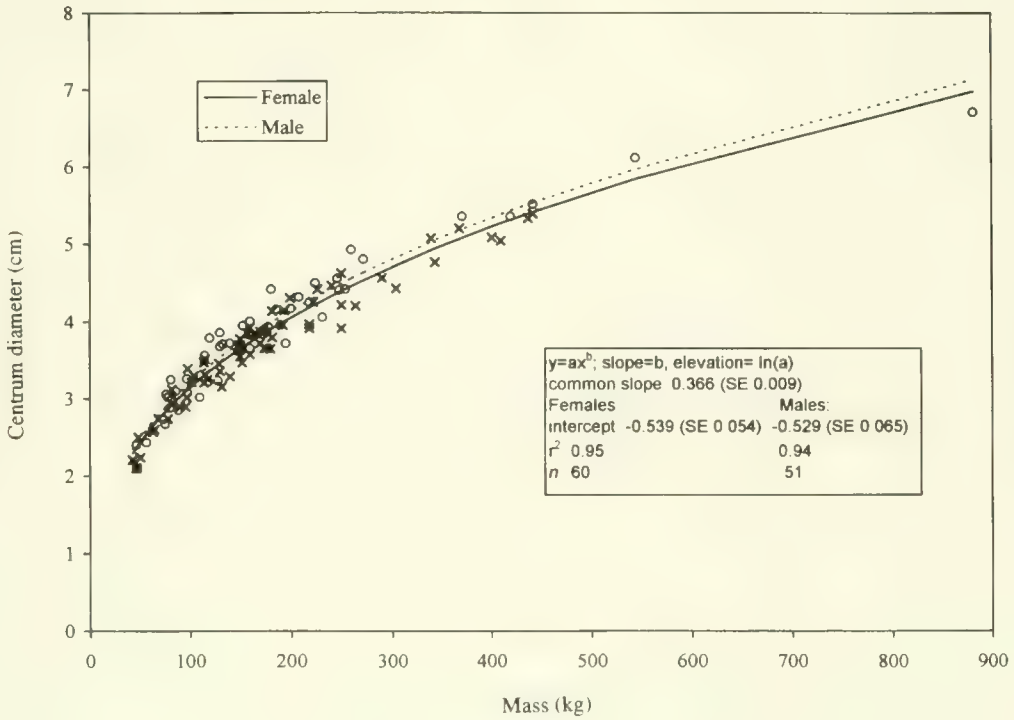

Figure 4

Relationship between centrum diameter and mass for female (x) and male (o) white sharks, *C. carcharias*. Squares indicate shark BT433 at tagging and recapture.

Table 6

Observed and back-calculated mass at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed mass (kg)					Back-calculated mass (kg)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	42	42	42		1	14	36	22	4	112
1	46	97	69	19	11	18	120	48	17	110
2	68	199	120	37	18	33	198	85	31	98
3	81	218	139	35	25	55	256	124	44	76
4	98	250	176	42	26	73	352	164	55	46
5	112	368	234	68	15	90	280	188	48	22
6	218	442	314	84	7	186	313	239	42	13
7	272	442	386	77	4	238	416	310	55	10
8	371	437	404	47	2	351	406	380	23	5
9	—	—	—	—	—	420	504	452	45	3
10	544	544	544	–	1	506	625	565	84	2
11	—	—	—			618	618	618	—	1
12	—	—	—	—	—	685	685	685	—	1
13	882	882	882	—	1	751	751	751	—	1
14	—	—	—	-	—	859	859	859	—	1

(χ^2 test, $P<0.001$, $n=22$). With method SC-A, and again only with vertebrae where all three counts had the same last band, the observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=75$), again irrespective of whether opaque band deposition was

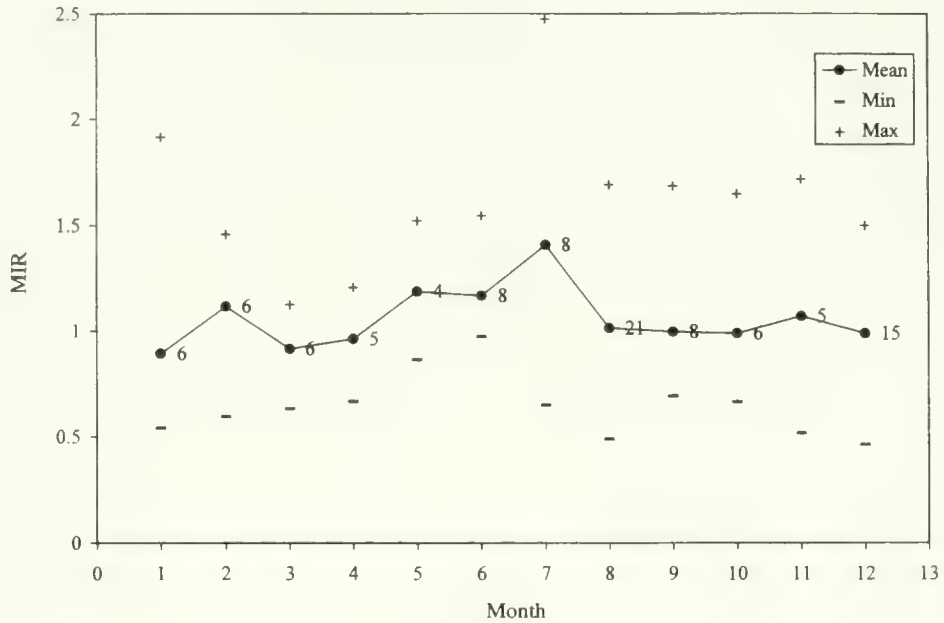

Figure 5

Marginal increment ratio (MIR) by month for the white shark, *C. carcharias*. Numbers indicate sample size, vertical bars indicate the standard error of the mean, and +/– indicates the range. Measurements were obtained by using method SC-A. 1 = January, 12 = December.

assumed to occur in summer or in winter. The exclusion of borderline cases, however, resulted in a significant difference between observed and the expected ratios (χ^2 test, $P<0.001$, $n=39$), assuming opaque band deposition in summer, but no significant difference (χ^2 test, $P>0.05$, $n=39$), assuming a translucent band deposition in summer.

The vertebra of shark BT433 was difficult to read (Fig. 1B), when compared with other sharks of similar length and mass (Fig. 1A). For this reason, we also examined the vertebra with transmitted light (Wintner and Cliff, 1996), and our interpretation of GRs is based mainly on this method. The OTC marker was visible in the opaque band (injected 30 October 1994). The deposition of OTC when injected intramuscularly occurs after a couple of weeks (Holden and Vince, 1973) or 21–35 days (Brown and Gruber, 1988). The opaque band would therefore have been deposited in summer (November or December). The last band in the vertebra was an opaque band. Because the shark was recaptured on 27 May 1997 (the beginning of winter), the translucent band might have been in the process of being formed.

MIR analysis of the entire sample (Fig. 5), however, did not show a distinct time of GR formation because mean and minimum ratios did not get close to zero. The results of a Kruskal-Wallis analysis indicated that there is no relation between MIR and month ($P=0.39$). In view of the results from the above recaptured shark and if the peak in July was regarded as a single peak, we assumed that one GR was formed annually, combined with the minimum MIR trend. With the latter, GR formation may occur during December or January. Because of the ambiguity of the results of the centrum analyses, however, annual periodicity of GR could not be confirmed.

Age and growth

The von Bertalanffy growth function was the most appropriate model for the data sets obtained by both methods SC-A and XR-A. The length-GR data set obtained by method SC-B was not investigated further because two growth models, Putter no. 2 and Gompertz (Punt and Hughes, 1989), provided a better fit than did the von Bertalanffy growth function. In addition, the L_∞ values obtained by the two models were too low to be realistic according to observed sizes of white sharks. Sexes could not be compared because there were no females larger than 300 cm; consequently no meaningful von Bertalanffy growth function could be fitted. Although the VBGP for the two methods SC-A and XR-A differed, there was little difference in the calculated GR over the range of lengths sampled (Fig. 6). Method SC-A had lower relative standard errors and a more realistic L_∞ than

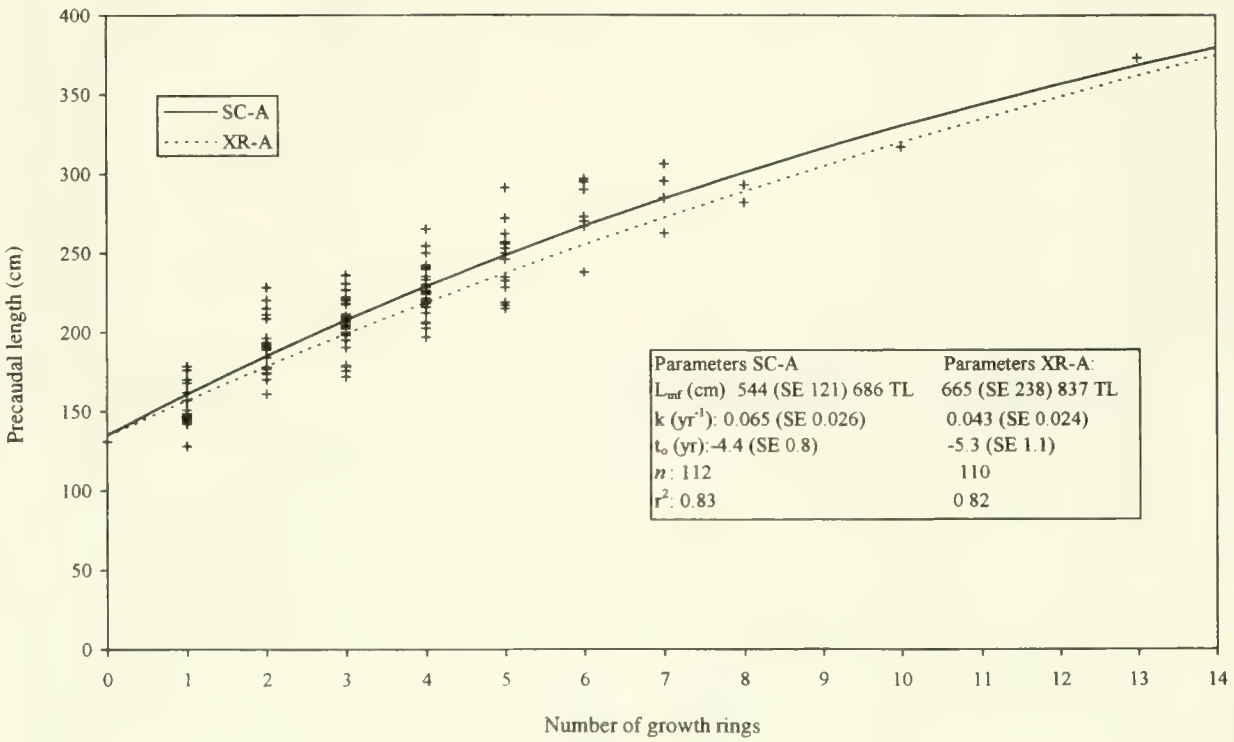

Figure 6

Von Bertalanffy growth curves and parameters for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using methods SC-A and XR-A. Observed values (+) are those for the method SC-A. Squares indicate shark BT433 at tagging and recapture.

method XR-A. For these reasons the results of the former method were used for back-calculations, MIR analysis, fitting of the Gompertz growth curve, growth calculations, and GR estimates.

Table 7 shows the number of GRs counted for various animals. The largest female, an adolescent, (297 cm) had 6 GRs; there were no mature females. Of the three mature males, the smallest had 8 GRs (293 cm), the other two had 10 and 13 GRs (317 and 373 cm), respectively. Size at birth ranged between 100 cm (back-calculated value) and 135 cm (predicted value). Shark BT433 was found to have one GR at tagging (140 cm) and three GRs at recapture (209 cm), after 2.6 yr at liberty (Fig. 1B; Fig. 6).

Table 7

Growth ring (GR) counts for animals of certain lengths (PCL, cm) or certain mass (kg).

	Male			Female		
	No. of GRs	PCL	mass	No. of GRs	PCL	mass
Lowest number of GRs	1	142	56	0	131	42
Highest number of GRs	13	373	882	8	282	437
Smallest animal	1	142	46	1	128	42
Largest animal	13	373	882	6	297	442
Smallest mature animal	8	293	371	—	—	—

A Gompertz growth curve was fitted to the mass-GR data (Fig. 7). The female and male with the highest number of GRs, had 8 GRs (437 kg) and 13 GRs (882 kg), respectively (Table 7). Mass at birth ranged between 22 kg (back-calculated value) and 54 kg (predicted value).

Mean growth rates calculated from observed lengths were higher overall than those calculated from predicted lengths (Fig. 8). Mean growth for predicted lengths was 26 cm for the period 0–1 GR, decreasing to 20 cm (4–5 GRs), 16 cm (7–8 GRs), and 12 cm (12–13 GRs). Mean observed growth in mass was also higher than that of predicted values (Fig. 8). Mean growth for predicted mass was 23 kg for 0–

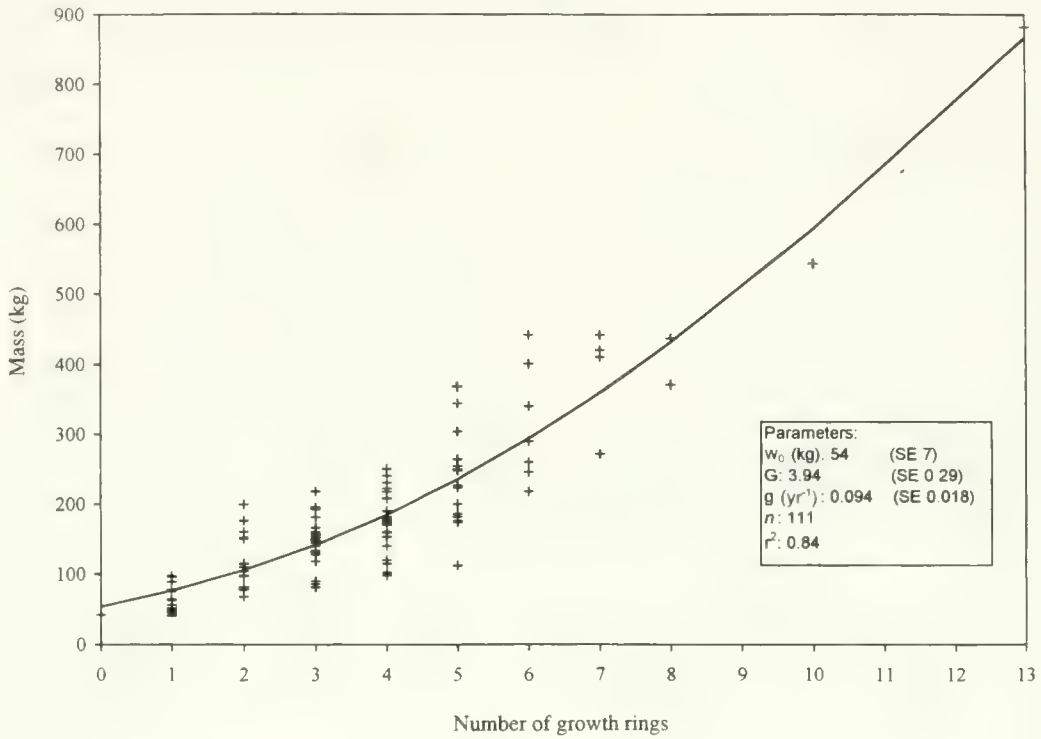

Figure 7

Gompertz growth curve for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using method SC-A. Squares indicate shark BT433 at tagging and recapture.

1 GR, increasing to 51 kg (4–5 GRs), 78 kg (7–8 GRs) and 94 kg (12–13 GRs). Shark BT433 grew 69 cm and 104 kg in 2.6 years (Fig. 1B) which represents a mean annual growth of 27 cm and 40 kg.

Discussion

Annual GR periodicity has been partly verified for several species (Cailliet, 1990). For some species of the family Lamnidae, biannual GR periodicity has been reported. Parker and Stott (1965) used the mean length of 17 *Cetorhinus maximus* sampled in winter and 15 sampled in summer and treating them as age classes, derived a tentative growth curve. They stated that their growth curve derived from ring counts of five vertebrae was similar to the first one when a deposition of two GRs per year was assumed. They were, however, careful to note that there was "nothing to indicate beyond doubt that the addition of two rings is the direct result of the passage of an annual seasonal cycle" and said that several findings did not "harmonise with the idea of annual increase of two rings."

Pratt and Casey (1983) determined age and growth of *Isurus oxyrinchus* from the Atlantic by length-month analysis, length-frequency analysis, tag-recapture information, and vertebral ring counts. The results of the first analysis were used to interpret the accuracy of the other methods. Their growth curve for *I. oxyrinchus,* based on back-calculated sizes, agreed closely with those obtained by the other methods if biannual ring deposition was assumed. The vertebrae from four noninjected recaptured *I. oxyrinchus*, however, gave inconclusive results because two supported annual and the other two biannual GR deposition. Pratt and Casey stated that "vertebral rings may thus yield an approximation of age, accurate in the smaller sizes where estimates have been correlated with other methodologies. Adults may not lay down yearly, and it is possible that we have underestimated their age, but we have no data to support this possibility."

Cailliet et al. (1983a) assumed annual GR deposition in *I. oxyrinchus* from California waters. Their growth rate estimates, based on tag-recapture analysis, were therefore half of those of Pratt and Casey (1983) and had a much smaller variation in the estimate. Cailliet et al. (1983a) stated that although "this discrepancy could be related to differences in habitat or environmental conditions or differences in

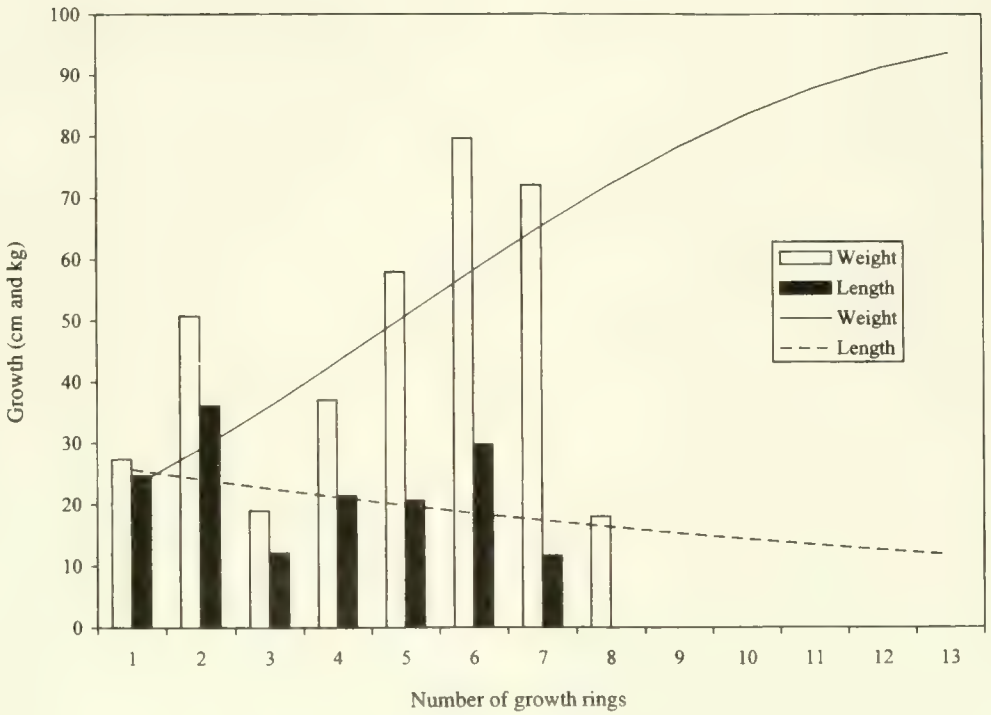

Figure 8

Observed (bar) and predicted (line) growth in mass and length per growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained by using method SC-A.

sample size or ageing methodology" it was interesting to note "that the growth rate reported by Pratt and Casey (1983) based on their back-calculation from counts of bands on centra, would be similar to ours if each pair of bands from their fish were interpreted as an annual event."

Cailliet et al. (1985) assumed annual GR periodicity in their age and growth study of *C. carcharias*. As with the studies mentioned above, MIR analysis could not be included to validate the temporal periodicity of the GRs. The only lamnoid study to have done so, apart from this one, was that of Branstetter and Musick (1994) on *Carcharias taurus,* which suggested a semiannual periodicity of band and ring formation. However, samples from three winter months were lacking. They also used a "odd-even ring count analysis" to verify this suggestion.

The results of the MIR analysis (Fig. 5) were inconclusive and did not confirm the results from shark BT433. Considerable time was spent on this analysis and great care was taken to discern the last deposited band in order not to overlook a recently formed band. Several vertebrae were remeasured, resulting only in removing the peaks of the curve and not in a reduction of the minimum MIR. Examination of the relative frequency of vertebrae with large MIR to those with low MIR plotted against month (Batista and Silva, 1995) did not shed light on this issue. Annual or biannual GR periodicity for *C. carcharias* could not be confirmed in this study by two centrum edge analyses.

There seems to be some unexplained variation in GR deposition among lamnoids, which is further compounded by our study. Pratt and Casey (1983) stated that in *I. oxyrinchus* instead of the traditional annual ring deposition "a more likely cause for ring formation would be times of stress or deprivation such as migration and mating." Similarly, Branstetter and Musick (1994) suggested that in *C. taurus* the formation of semiannual bands may reflect their north-south seasonal migration pattern, which is prompted in part by changing light and temperature patterns. There is currently not enough evidence to prove a similar migration pattern for *C. carcharias* in South African waters (Cliff et al., 1996a, 1996b).

Traditionally, ages of sharks have been related to length (Cailliet et al., 1983b; Cailliet et al., 1986). Natanson and Cailliet (1990) found that band deposition in *Squatina californica* was not annual but related to somatic growth. We therefore decided to fit a Gompertz growth curve because this curve usually describes the relationship between mass and age

well (Ricker, 1975). The curve did not show the typical asymmetrical sigmoid curve but seemed to approach an upper asymptote (Gulland, 1983). It was the method with the lowest relative standard errors for all parameters. Although there is also considerable variation in mass at GR, we felt that the Gompertz growth curve has merit, especially because there is a large change in mass associated with a small increase in length among large sharks. The results of the MIR analysis could be interpreted such that GR formation is not related to time of year but to mass increase (some sharks taking a longer time than others to gain the same amount of mass).

Typically, opaque band deposition is associated with summer growth (Cailliet et al., 1983b, 1986; Kusher et al., 1992), and the nature of the last deposited band can be related to the month of capture to verify this. Using method SC-A and only summer and winter months, we found that the observed ratio of translucent to opaque last bands did not differ significantly from the expected ratio, assuming a translucent band deposition in summer. When we used nine ring counts, however, the analysis did not show any relation between the nature of the last band and season. The analysis could be considered statistically weak owing to the low sample size but was included to emphasize the accuracy of the last band identification. In this study the band immediately after the angle change was opaque in most vertebrae, which is in keeping with Francis (1996) who reported time of parturition of white sharks as spring or summer. In addition, if our interpretation of vertebral bands in shark BT433 is correct, the opaque band would be formed in summer. Because of the inconclusive results of the centrum analyses of the entire sample, however, more recaptures of sharks injected with OTC are needed to confirm this theory.

The relation between centrum diameter and shark length was linear, as was found in *C. carcharias* by Cailliet et al. (1985) and in several other shark species (Cailliet et al., 1983b; Schwartz, 1983; Branstetter, 1987). For another species of the family Lamnidae, *I. oxyrinchus,* Pratt and Casey (1983) found a slightly curvilinear relationship for both females and males. The relation between centrum diameter and mass was multiplicative, which explains the slightly bigger difference in centrum diameter between the sexes than in the relation between centrum diameter and length. The differences between the sexes in both relationships, however, are slight and are probably not of biological significance.

Back-calculated mass and length values were lower than observed values. The differences between mean observed length (or mass) and mean back-calculated length (or mass) at each GR would decrease substantially if the observed GR 0 were treated as GR 1. This could be an indication that the angle change of the corpus calcareum is not formed at birth but in the first summer growth (Brown and Gruber, 1988; Wintner and Cliff, 1996).

X-radiography to enhance the visibility of GRs in elasmobranch vertebrae has been used successfully on several species (Cailliet et al., 1983a, 1983b; Yudin and Cailliet, 1990; Ferreira and Vooren, 1991). This technique was also used in the only other ageing study of *C. carcharias* by Cailliet et al. (1985). They counted GRs directly from x-radiographs and used silver nitrate staining to corroborate counts of larger vertebrae that proved more difficult to read. In our study, scanned images allowed for easy and rapid counts of rings and measurements for back-calculations. In addition, scanned images were easier to interpret because they showed less detail of the narrow circuli and prebirth marks than did the x-radiographs.

Prebirth marks in placental species are normally attributed to the time of placenta formation and attachment (Casey et al., 1985; Branstetter, 1987; Branstetter and Stiles, 1987). In our study, prebirth marks were found in *C. carcharias* vertebrae. No comments on prebirth marks in *C. carcharias*, *I. oxyrinchus,* or *Alopias vulpinus* were made by Cailliet et al. (1985), Pratt and Casey (1983), and Cailliet et al. (1983a), respectively. Branstetter et al. (1987) did not find prebirth marks in *Galeocerdo cuvier*, another aplacental species. Branstetter and Musick (1994), however, found prebirth marks in their *Carcharias taurus* specimens and related the first consistent prebirth ring to the size of the embryo when digestion of the large quantities of eggs begins. We did not relate prebirth marks to embryonic length using back-calculations because they represent growth in utero.

The APE indices for the three methods (5.3–6.1%) were considered acceptable. They were lower than those of the four methods used by Wintner and Cliff (1996) for *Carcharhinus limbatus* (8.1–13.0%, n=80–87) and those of Cailliet et al. (1990) who used "bow tie" sections of *Mustelus manazo* (6.9–12.7%, n=28–30). D-values (3.9–4.1%) were also considered to be acceptable because they were similar to those of Natanson and Kohler (1996) for *C. obscurus* (3,3%, n=42) and lower than those of Cailliet et al. (1990) (6.8–12.7%, n=27–30).

Age and growth estimates

Only one shark injected with OTC was recaptured (BT433). Although it was at liberty for an adequate time period, an interpretation of the bands on the x-radiograph was difficult, and therefore the results were based mainly on viewing the vertebra with

transmitted light. The number of GRs counted, however, were the same with these two methods and for both authors. While at liberty, the shark's mean annual growth increment was 28 cm and 42 kg. Francis (1996) reported size at birth between 92 and 116 cm and weight at birth between 12 and 32 kg and given that this shark was 140 cm and 46 kg at tagging, it is reasonable to assume that its age was in the region of one year. This estimation was confirmed by the OTC marker being visible at the edge of the first GR (Fig. 1B).

Table 8

Comparison of von Bertalanffy growth parameters. The bold values were obtained by refitting the data.

	Our study (SC-A)	Cailliet et.al (1985)	
		Their results	Refitted excluding 3 large animals
Range PCL	128–373	110–434	110–394
Range TL	165–472	129–508	129–461
VBGP			
L_∞	544 (686 TL)	653 (764 TL)	569 (666 TL)
SE	121	**134 (157 TL)**	110 (129 TL)
k	0.065	0.058	0.072
SE	0.026	**0.023**	0.028
t_0	–4.4	–3.5	–3.3
SE	0.8	**0.72**	0.72
n	112	21	18
r^2	0.83	**0.98**	0.97

Because we counted three GRs at recapture, the mean predicted growth/GR in the period from 1 to 3 GRs was 24 cm/GR and 33 kg/GR (Fig. 8). Assuming that one GR is deposited per year, the total growth of shark BT433 would be 62 cm and 86 kg in the period of 2.6 years. If the GR deposition is biannual, which is not impossible given the difficulty in interpreting this vertebra (Fig. 1B), the mean predicted growth would be 18 cm/GR and 32 kg/GR; this would amount to a total growth in a period of 2.6 yr (5.2 GR) of 94 cm and 166 kg. Because BT433 grew 69 cm and 104 kg, the first of these two predictions fits the observed growth better than the second.

Further evidence to support the hypothesis of annual GR deposition can be found in Figures 6 and 7. If the number of GRs represents years, the expected size and mass of shark BT433 at tagging and recapture after 2.6 years is in accordance with the observed values of our sample (Fig. 6). Assuming biannual GR deposition, we believe the shark's size and mass at tagging is still in accordance with the observed values (Fig. 7); however, it would have been in the region of 288 cm and 375 kg at recapture. Because evidence of annual GR deposition in *C. carcharias* is based on the recapture of a single shark injected with OTC and because our centrum analyses neither confirmed nor contradicted annual ring deposition, the discussions below are based on number of GRs rather than years.

Our VBGPs, in the absence of very large sharks, were L_∞ = 544 cm (SE 121), k = 0.065/yr (SE 0.026), and t_0 = –4.4 yr (SE 0.8). We fitted a von Bertalanffy growth curve to the data points presented by Cailliet et al. (1985) in order to compare standard errors (Table 8). The results were very similar, but given the larger sample size in our study, it would appear that there is greater variation in length at number of GRs in *C. carcharias* from South Africa.

Our largest shark (373 cm) measured 452 cm TL. The absence of larger sharks in our study undoubtedly accounts for the lower L_∞ of 544 cm (686 cm TL), as opposed to that of Cailliet et al. (1985) of 654 cm (764 cm TL). This finding was confirmed when the three markedly larger sharks (494–508 cm TL) of their study were omitted and the recalculated L_∞ was 569 cm (666 cm TL) (Table 8). The conversion of the original data of Cailliet et al. (1985) from TL to PCL had no effect on the VBGP and their standard errors. One should keep in mind, however, that comparisons of L_∞ are somewhat hampered by the fact that TL length is measured in two different ways (Mollet et al, 1996) by various authors, although the difference in *C. carcharias* is not as pronounced as, e.g., in members of the family Carcharhinidae.

The maximum size attained by the white shark is the subject of much interest and controversy and, more importantly, uncertainty (Ellis and McCosker, 1991). Randall (1973, 1987) refuted the lengths of 1113, 900, and 640 cm TL attributed to *C. carcharias*. According to him, the largest reliable measured white shark is 513 cm (600 cm TL). Mollet et al. (1996) calculated the size of two large white sharks, using three morphometric measurements, at 453–701 cm (530–820 cm TL) and 393–598 cm (460–700 cm TL), respectively. These results were consistent with the estimated TL of >700 and 700 cm, respectively. They concluded that the most solid TL estimates for these two sharks were those original estimates. Our L_∞ is larger than the shark from Randall and is smaller than the data of Mollet et al. (1996) and Cailliet et al. (1985).

Our growth coefficient is similar to that found by Cailliet et al. (1985), and both are an order of magnitude lower than that of *I. oxyrinchus* at 0.203–0.266 (Pratt and Casey, 1983) and that of *Lamna nasus* at 0.116 (Aasen, 1963). In the first year of growth, *C. carcharias* grows 19–26% of its size at birth which is less than that of other lamnoids (Branstetter, 1990). Our findings place *C. carcharias* in Branstetter's (1990) group of sharks with slow growth (k<0.10; growth in the first year<30% of the birth size).

In our study, back-calculated size at birth was 100 cm and calculated value was 135 cm. The smallest accurately measured free-swimming *C. carcharias* in southern Africa was 108 cm (140 cm TL) (Smith, 1951) and the sizes of the smallest white sharks caught at the NSB are 128–145 cm. "Umbilical scars" (Cliff et al., 1996a) were present in sharks of 138, 143, 144, and 145 cm, including the 131 cm (0 GR) specimen of this study. If the presence of these scars is interpreted as an indication of recent birth, it is tempting to suggest a very wide range in size at birth, between 100 and 145 cm. These scars, however, may persist for some time after birth and given a growth of about 25 cm/yr in newborn sharks, birth size of *C. carchirias* would be more in the region of that reported by Francis (1996), i.e. 92–116 cm (120–150 cm TL). Our range in mass at birth (22–54 kg) is also substantial, which is in keeping with Francis (1996) who stated that the range in mass at birth for *C. carcharias* is quite pronounced.

Our three mature males had 8, 10, and 13 GRs (293, 317, and 373 cm; 371, 544, and 882 kg, respectively). The NSB has caught immature specimens larger and heavier than our smallest mature, e.g. a 295 cm (420 kg) and a 306 cm (442 kg) specimen (Cliff et al., 1996a). Pratt's (1996) smallest mature male was 299 cm (379 cm TL), which is similar to our shark; however, he notes that sizes at sexual maturity for male *C. carcharias* vary widely in the literature. These differences could be due to a variation in length at maturity depending on location, both compounded by the use of different length conversion equations and maturity criteria. If the number of GRs is taken as an age estimate, assuming annual GR deposition, male *C. carcharias* in South Africa would mature between 8–10 years which is similar to the findings of Cailliet et al. (1985) who worked with a size at maturity of 313–365 cm (366–427 cm TL), corresponding to an age of 9–10 years. This age at maturity is higher than that of other lamnids, e.g. that of male *I. oxyrinchus* at 2–3 years (Pratt and Casey, 1983) and male *L. nasus* at about 5 years (Paust and Smith, 1986).

No mature female has ever been examined from NSB nets, and the biggest female in our study was 297 cm (6 GRs). The biggest female on record is an immature 348 cm specimen (Cliff et al., 1989), and Bass et al. (1975) reported a mature female of 352 cm (445 cm TL). Again if GRs are deposited annually, the above specimens would be 11 and 12 years, respectively. Age at maturity for female *C. carcharias* in South Africa would then be at least 12–13 years, slightly higher than that for males. Again, this age at maturity is higher than in other lamnids, e.g. that for female *I. oxyrinchus* at 7 years (Pratt and Casey, 1983) and female *L. nasus* at 9–10 years (Paust and Smith, 1986).

Although this study could not conclusively prove annual or biannual GR periodicity, the recapture of one shark injected with OTC provided some evidence for annual GR deposition. Assuming that only one growth ring is laid down per year, then *C. carcharias* from South Africa is relatively slow growing in comparison with other lamnoids. This observation would support current protective legislation. The NSB nets are now the only directed source of apparent fishing mortality for *C. carcharias* in South Africa. Cliff et al. (1996b) were of the opinion, using their estimates of mortalities, that the current fishing mortality did not represent overfishing of the white shark stock. Examination of interannual catch rates of *C. carcharias* in the NSB nets showed an significant decline immediately following the introduction of netting, but thereafter (1978–93) there was no significant change (Cliff et al., 1996a). Because they are apex predators, *C. carcharias* are likely to have a small population size (Cliff et al., 1996b), and we have no knowledge about the fecundity and nursery grounds of this species in South African waters. Any possible relaxation of the South African current legislation will depend on improved knowledge about population size, immigration and emigration, natural mortality, and fecundity of *C. carcharias* from South Africa.

Any such relaxation, however, is highly unlikely given the increasing protection that has been granted to this species worldwide. It is now also protected in some states of America (Fergusson et al., in press) and Australia (Stevens[1]), where such legislation is based on a more limited knowledge or understanding of the biology and population dynamics of this species.

Acknowledgments

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Abstract.—Fish and other animals are often tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. Results of these studies are biased if tags are not retained permanently and if tag loss is not taken into account. In this paper, we develop a simple tag shedding model to account for the effects of time at liberty, sex, and other factors and use one of its special cases to estimate the instantaneous tag shedding rate from data based on two double-tagging experiments on the school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, off southern Australia. For either species, tag shedding rate could vary with tag type, position of tag on fish, and sex of fish, but not with length at release or time at liberty. The shedding rate of Petersen disc fin tags was well above 50%/yr. Dart tags were shed at a higher rate (41%/yr for school shark; 63%/yr for gummy shark) than either "Roto" or "Jumbo" fin tags (8%/yr for school shark; 6%/yr for gummy shark). For either species of shark, the shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of dart tags anchored in the dorsal musculature.

Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood

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Tags are markers placed on or in animals to identify an individual. Animals are tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. In many studies, a tagged animal is assumed to retain its tag permanently. This assumption, however, is not valid for certain types of tags. Consequently, many attempts have been made to estimate tag shedding rates (e.g. Davis and Reid, 1982; Francis, 1989; Faragher and Gordon, 1992; Treble et al., 1993; Hampton, 1996; Xiao, 1996a).

Tag shedding models are of three main types; all are based on Beverton and Holt's (1957, p. 205, equations 14.32–14.37) model for a double-tagging experiment. Some models are conditional on the number of recaptured fish with a single tag, as well as the number of recaptured fish with both tags as a function of time at liberty, and use the least squares method (Gulland, 1955, 1963; Chapman, 1961; Paulik, 1963; Chapman et al., 1965; Bayliff and Mobrand, 1972; Russell, 1980; Kirkwood, 1981; Alt et al., 1985) or more generally the maximum likelihood method (Robson and Regier, 1966; Seber, 1973; Seber and Felton, 1981; Wetherall, 1982; Kremers, 1988; Fabrizio et al., 1996) for estimation of parameters. Other models are conditional on the number of recaptured fish retaining at least one tag as a function of time at liberty and on the exact times at liberty (Wetherall, 1982). Use of these types of models in data analysis requires grouping recaptured fish by time at liberty because of an insufficient number of recaptures for a particular (exact) time at liberty, especially in small-scale tagging experiments. Still other models are conditional only on the exact times

at liberty (Kirkwood and Walker, 1984; Hampton and Kirkwood, 1989; Hearn et al., 1991; Xiao, 1996a). These models 1) use the exact times at liberty in model fitting, 2) use probabilities of tag retention directly rather than using the often statistically undesirable ratios as the dependent variable in regression analysis, 3) apply to both small (but see below) and large numbers of recaptures, and 4) yield estimates of tag shedding rates independent of instantaneous fishing mortality, natural mortality, and mortalities due to all other causes. Almost all previous tag shedding models have considered only the effects of fish time at liberty on shedding rates, ignoring effects of other equally or potentially more important factors, such as fish sex and size.

School shark *Galeorhinus galeus* (Linnaeus) and gummy shark *Mustelus antarcticus* (*sensu* Last and Stevens, 1994) are major species in the Australian southern shark fishery—a commercial fishery that extends from Western Australia through South Australia to Bass Strait and Tasmania in the east and that has an annual landed value of $A15.6 million (Walker et al., 1996). Two tagging studies were undertaken to study the growth (Moulton et al., 1992), natural mortality (Grant et al., 1979), and local movements of these two species within Bass Strait and off eastern Tasmania (T. I. Walker, Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic 3225 Australia, unpubl. data). These studies suggest that school shark are highly migratory, compared with gummy shark, but they provide little quantitative information about their rates of movements beyond these areas, where most sharks were tagged and released. Also, fishing effort was too poorly documented at the time of Grant et al.'s (1979) tagging program (1940s and 1950s) to be adequate for quantifying the rates of movement for these two species. Finally, predominant use of gill nets with large mesh sizes (8 inches) off the southern coast of Western Australia and off South Australia at the time of T.I. Walker's tagging study (1970s) led to a low level of fishing effort and a small number of recaptures. Such a lack of quantitative information on rates of movement hampered stock assessment. Consequently, a large-scale tagging experiment was designed (Xiao, 1996b) and implemented to fill in this gap. In that study, thousands of individuals were released; each individual was tagged with an easily attachable and highly visible external tag (a Roto tag or a dart tag), the shedding rate of which was to be determined through an accompanying double-tagging experiment (see below).

In this paper, we develop a simple tag shedding model to account for the effects of fish sex, size, and factors other than time at liberty and use a special case to estimate the instantaneous tag shedding rate for the two species of sharks.

Materials and methods

Tagging experiments

Two double-tagging experiments were performed on *G. galeus* and *M. antarcticus*. In the first experiment (Olsen, 1953; Walker, 1989; Table 1), a total of 2597 school and 363 gummy sharks with a respective total length range of 31–164 (85 ±43, n=2586) cm and 32–179 (102 ±24, n=362) cm were captured by longline hooks, measured to the nearest centimeter, tagged with an internal and external tag, and released in inshore waters off Victoria, South Australia, and Tasmania, Australia, from 22 May 1949 to 10 July 1954. Internal tags were either 50 mm long and 23 mm wide (J-tag), or 50 mm long and 22 mm wide (L-tag), or 35 mm long and 10 mm wide (S-tag) and were inserted into the body cavity through an incision on the left flank parallel to the muscles in the lower half of the body immediately below the posterior half of the first dorsal fin. External tags were a white (W-tag) or gray Petersen disc (G-tag); both were 16 mm in diameter and 1 mm thick and were placed in the midcentral part of the first dorsal fin. Of those released, 417 school and 20 gummy sharks were recaptured within 42.5 years. Their respective total length at recapture ranged from 43 to 175 (127 ±35, n=267) cm and from 83 to 152 (125 ±19, n=12) cm; their respective times at liberty ranged from 31 to 15,510 (2761 ±2758, n=417) d, and from 52 to 3900 (1771 ±1159, n=20) d.

In the second double-tagging experiment (Table 2), as part of a major tagging experiment (see above), 291 school and 731 gummy sharks with a respective total length range of 38–168 (134 ±17, n=291) cm and 40–176 (108 ±20, n=729) cm were captured in gill nets, measured to the nearest millimeter, tagged with two external tags (a Roto tag and a dart tag) either in the lower half or basal cartilage of the first dorsal fin, and released off southern Australia, from 15 December 1993 to 24 April 1996. Two types of Roto tags were used: either a 45-mm-long and 18-mm-wide Jumbo (Roto) tag, or a 36-mm-long and 9-mm-wide Roto tag (Daltons of New South Wales, Australia). The dart tag was 95 mm long and 2 mm in diameter (Hallprint of South Australia, Australia). As of 1 May 1997, 48 school and 207 gummy sharks were recaptured. Their respective total length at recapture ranged from 85 to 179 (135 ±18, n=38) cm and from 66 to 167 (115 ±17, n=150) cm; their respective times at liberty ranged from 31 to 633 (269 ±163, n=48) d, and from 1 to 1138 (275 ±244, n=207) d.

Table 1

Description of the first double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable.

Row	Species	Tag A	Tag B	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	L-tag	W-tag	M	11	110 ±07	99–122	—	—	—	—	—
2	gummy	L-tag	W-tag	F	1	90 ± –	90–090	—	—	—	—	—
3	gummy	L-tag	G-tag	M	128	108 ±12	79–144	6(0,6,0)	131 ±16	114–145	2224 ±1154	1209–3900
4	gummy	L-tag	G-tag	F	129	112 ±20	77–179	13(0,13,0)	128 ±15	106–152	1698 ±1104	80–3531
5	gummy	S-tag	W-tag	M	32	86 ±28	33–136	—	—	—	—	—
6	gummy	S-tag	W-tag	F	14	65 ±20	38–102	—	—	—	—	—
7	gummy	S-tag	G-tag	M	27	88 ±22	39–119	1(0,1,0)	83 ±–	83–083	52 ± –	52–52
8	gummy	S-tag	G-tag	F	21	63 ±25	32–117	—	—	—	—	—
9	school	J-tag	W-tag	M	59	127 ±26	62–154	18(2,15,1)	146 ±11	125–155	5039 ±4369	705–15251
10	school	J-tag	W-tag	F	41	128 ±33	60–164	14(1,13,0)	152 ±15	113–167	3260 ±2333	319–8380
11	school	L-tag	W-tag	M	32	145 ±07	116–160	7(1,6,0)	155 ±14	143–174	4382 ±3142	841–9539
12	school	L-tag	W-tag	F	15	148 ±15	106–160	4(0,4,0)	161 ±08	155–167	3809 ±5548	546–12114
13	school	L-tag	G-tag	—	4	137 ±18	112–155	2(0,2,0)	152 ±–	152–152	2971 ±0769	2427–3515
14	school	L-tag	G-tag	M	521	141 ±12	71–163	127(4,123,0)	147 ±12	114–175	3858 ±3100	82–15510
15	school	L-tag	G-tag	F	292	137 ±17	73–164	71(6,65,0)	149 ±12	112–167	3142 ±2341	89–9107
16	school	S-tag	W-tag	—	2	67 ±09	60–073	—	—	—	—	—
17	school	S-tag	W-tag	M	14	48 ±06	40–057	2(0,2,0)	83 ±–	83–083	2652 ±2456	915–4389
18	school	S-tag	W-tag	F	14	54 ±06	43–065	5(0,5,0)	107 ±40	57–141	2566 ±1944	260–5262
19	school	S-tag	G-tag	—	15	57 ±12	32–067	2(1,1,0)	—	—	377 ±0434	70–684
20	school	S-tag	G-tag	M	781	54 ±13	31–148	86(7,79,0)	97 ±35	43–159	1568 ±1604	31–7555
21	school	S-tag	G-tag	F	807	53 ±12	31–148	79(13,64,2)	95 ±33	51–159	1221 ±1512	35–6200

Table 2

Description of the second double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable; tagging position refers to tag B's position.

Row	Species	Tag A	Tag B	Tagging position	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	Jumbo	dart	fin	M	68	115 ±08	97–140	13(9,3,1)	117 ±08	107–130	192 ±119	64–386
2	gummy	Jumbo	dart	fin	F	66	125 ±21	80–176	19(17,1,1)	122 ±10	108–145	119 ±083	13–309
3	gummy	Jumbo	dart	muscle	M	101	109 ±14	87–144	41(22,19,0)	112 ±14	86–148	278 ±232	5–818
4	gummy	Jumbo	dart	muscle	F	164	119 ±21	68–175	43(19,24,0)	123 ±20	91–167	340 ±273	6–1138
5	gummy	Roto	dart	muscle		1	106 ± –	106–106	1(0,1,0)		—	83 ± –	83–83
6	gummy	Roto	dart	muscle	M	151	96 ±18	45–135	37(20,15,2)	106 ±17	66–148	309 ±262	2–1059
7	gummy	Roto	dart	muscle	F	180	99 ±18	40–136	53(26,26,1)	112 ±14	78–138	278 ±256	1–886
8	school	Jumbo	dart	fin	M	46	135 ±14	108–168	3(3,0,0)	136 ±13	123–149	136 ±089	34–202
9	school	Jumbo	dart	fin	F	81	139 ±12	108–167	15(11,3,1)	141 ±12	110–157	306 ±130	123–546
10	school	Jumbo	dart	muscle	M	77	134 ±11	100–158	12(9,2,1)	140 ±20	107–179	263 ±201	33–633
11	school	Jumbo	dart	muscle	F	53	140 ±14	100–164	9(6,3,0)	142 ±10	122–155	272 ±179	31–551
12	school	Roto	dart	muscle	M	13	108 ±23	71–152	3(3,0,0)	110 ±22	85–124	317 ±164	146–474
13	school	Roto	dart	muscle	F	21	110 ±29	38–160	6(2,4,0)	115 ±15	100–136	229 ±172	34–468

Model

Consider a (single) fish i that is captured, double tagged, and released at time $t_0(i)$. The index i can be used to examine the effects of any factor on the instantaneous tag shedding rate. Let A and B indicate the two types of tags and

$P(i,A,B,t(i))$ = probability of retaining both tags at time $t(i)$;
$P(i,A,0,t(i))$ = probability of retaining only tag A at time $t(i)$;
$P(i,0,B,t(i))$ = probability of retaining only tag B at time $t(i)$;
$P(i,0,0,t(i))$ = probability of retaining neither tag at time $t(i)$;
$\dot{C}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained both tags;
$\dot{C}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag A;
$\dot{C}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag B;
$\dot{C}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained neither tag;
$\dot{U}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained both tags;
$\dot{U}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag A;
$\dot{U}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag B;
$\dot{U}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained neither tag;
$\dot{D}(i,A,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained both tags;
$\dot{D}(i,A,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag A;
$\dot{D}(i,0,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag B;
$\dot{D}(i,0,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained neither tag;
$\pi(i)$ = probability that it remains alive after type-I mortality (i.e. mortality due to the immediate effects of tagging and handling);
$\rho(i,j)$ = probability that it retains tag j (j=A,B) after type-I shedding (i.e. tag shedding due to the immediate effects of tagging and handling);
$F(i,t(i))$ = instantaneous rate of fishing mortality at time $t(i)$;
$M(i,t(i))$ = instantaneous rate of natural mortality at time $t(i)$;
$R(i,A,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained both tags;
$R(i,A,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag A;
$R(i,0,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag B;
$R(i,0,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained neither tag;
$\lambda(i,A,t(i))$ = instantaneous shedding rate of tag A at time $t(i)$; and
$\lambda(i,B,t(i))$ = instantaneous shedding rate of tag B at time $t(i)$.

We assume that, in the time interval $[t(i),t(i)+\Delta t]$, the probability that fish i retaining both tags is caught is $F(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it is dead is $M(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it sheds tag A is $\lambda(i,A,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, and the probability that it sheds tag B is $\lambda(i,B,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, where $O(\Delta t)\to 0$ as $\Delta t\to 0$. It is also assumed that these events are independent with no more than one event occurring in the time interval. Under these assumptions, the probability that fish i retains both tags at time $t(i)+\Delta t$ given that it has retained both tags at time $t(i)$ is given by

$$P(i,A,B,t(i)+\Delta t)=[1-F(i,t(i))\Delta t-M(i,t(i))\Delta t-\lambda(i,A,t(i))\Delta t-\lambda(i,B,t(i))\Delta t]\,P(i,A,B,t(i))+O(\Delta t).$$

Taking the limit $\Delta t\to 0$ and letting the dot above a quantity denote the first derivative of that quantity with respect to $t(i)$ yields

$$\dot{P}(i,A,B,t(i))=-[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))]\,P(i,A,B,t(i)).$$

This and similar arguments yield a tag shedding model of the form

$$\begin{cases} \dot{P}(i,A,B,t(i)) = -\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))\right]P(i,A,B,t(i)) \\ \dot{P}(i,A,0,t(i)) = -\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))\right]P(i,A,0,t(i))+\lambda(i,B,t(i))P(i,A,B,t(i)) \end{cases} \quad (1)$$

$$
\begin{cases}
\dot{P}(i,0,B,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,B,t(i))\right]P(i,0,B,t(i)) + \lambda(i,A,t(i))P(i,A,B,t(i)) \\
\dot{P}(i,0,0,t(i)) = -\left[F(i,t(i)) + M(i,t(i))\right]P(i,0,0,t(i)) + \lambda(i,A,t(i))P(i,A,0,t(i)) + \lambda(i,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,A,B,t(i)) = F(i,t(i))R(i,A,B,t(i))P(i,A,B,t(i)) \\
\dot{C}(i,A,0,t(i)) = F(i,t(i))R(i,A,0,t(i))P(i,A,0,t(i)) \\
\dot{C}(i,0,B,t(i)) = F(i,t(i))R(i,0,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,0,0,t(i)) = F(i,t(i)) = R(i,0,0,t(i))P(i,0,0,t(i)) \\
\dot{U}(i,A,B,t(i)) = F(i,t(i))\left[1 - R(i,A,B,t(i))\right]P(i,A,B,t(i)) \qquad \left[t_0(i) \le t(i)\right] \\
\dot{U}(i,A,0,t(i)) = F(i,t(i))\left[1 - R(i,A,0,t(i))\right]P(i,A,0,t(i)) \\
\dot{U}(i,0,B,t(i)) = F(i,t(i))\left[1 - R(i,0,B,t(i))\right]P(i,0,B,t(i)) \qquad (1) \\
\dot{U}(i,0,0,t(i)) = F(i,t(i))\left[1 - R(i,0,0,t(i))\right]P(i,0,0,t(i)) \qquad \text{continued} \\
\dot{D}(i,A,B,t(i)) = M(i,t(i))P(i,A,B,t(i)) \\
\dot{D}(i,A,0,t(i)) = M(i,t(i))P(i,A,0,t(i)) \\
\dot{D}(i,0,B,t(i)) = M(i,t(i))P(i,0,B,t(i)) \\
\dot{D}(i,0,0,t(i)) = M(i,t(i))P(i,0,0,t(i))
\end{cases}
$$

with initial conditions

$$
\begin{cases}
P(i,A,B,t_0(i)) = \pi(i)\rho(i,A)\rho(i,B) \\
P(i,A,0,t_0(i)) = \pi(i)\rho(i,A)\left[1 - \rho(i,B)\right] \\
P(i,0,B,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\rho(i,B) \\
P(i,0,0,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\left[1 - \rho(i,B)\right] \\
C(i,A,B,t_0(i)) = 0 \\
C(i,A,0,t_0(i)) = 0 \\
C(i,0,B,t_0(i)) = 0 \\
C(i,0,0,t_0(i)) = 0 \\
U(i,A,B,t_0(i)) = 0 \\
U(i,A,0,t_0(i)) = 0 \\
U(i,0,B,t_0(i)) = 0 \\
U(i,0,0,t_0(i)) = 0 \\
D(i,A,B,t_0(i)) = 0 \\
D(i,A,0,t_0(i)) = 0 \\
D(i,0,B,t_0(i)) = 0 \\
D(i,0,0,t_0(i)) = 0
\end{cases}
$$

Solution of this system of ordinary differential equations as an initial value problem gives

$$
\begin{cases}
P(i,A,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}[\lambda(i,A,s)+\lambda(i,B,s)]ds} \\
P(i,A,0,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
P(i,0,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\
P(i,0,0,t(i)) = \pi(i)e^{\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
C(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,A,B,s)P(i,A,B,s)ds \\
C(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,A,0,s)P(i,A,0,s)ds \\
C(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,0,B,s)P(i,0,B,s)ds \\
C(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,0,0,s)P(i,0,0,s)ds \\
U(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,A,B,s)]P(i,A,B,s)ds \\
U(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,A,0,s)]P(i,A,0,s)ds \\
U(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,0,B,s)]P(i,0,B,s)ds \\
U(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,0,0,s)]P(i,0,0,s)ds \\
D(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,A,B,s)ds \\
D(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,A,0,s)ds \\
D(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,0,B,s)ds \\
D(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,0,0,s)ds
\end{cases}
\tag{2}
$$

This tag shedding model follows essentially the same line of thought as Xiao's (1996a) and can be readily phrased in the standard terminology of competing risks in survival analysis (David and Moeschberger, 1978). Also, notice that the left-hand side of Equation 1 sums to zero; the left-hand side of Equation 2 sums to $\pi(i)$.

When a single fish is double tagged and released at time $t_0(i)$, one of 16 mutually exclusive events can happen at time $t(i)$ (Equation 1 or 2). However, only three events are actually observable: the fish has, upon recapture, retained both tags, retained tag A and lost tag B, or lost tag A and retained tag B, with respective probabilities of $\dot{C}(i,A,B,t(i))$, $\dot{C}(i,A,0,t(i))$ and $\dot{C}(i,0,B,t(i))$. The event that it has shed both tags upon recapture, with a probability of $\dot{C}(i,0,0,t(i))$, cannot be observed, for when both tags are shed, a fish cannot be reliably distinguished from one that was never tagged. A likelihood function can be constructed to estimate parameters in Equation 1 or 2 by following arguments in standard competing risk analysis, but these estimates are substantially biased. To overcome this problem, we estimated model parameters by conditioning on observations of three events only, i.e. by maximizing the conditional likelihood function for all reported recaptures with at least one tag retained

$$L=L_1 \cdot L_2 \cdot L_3,$$

with

$$L_1 = \prod_{h=1}^{n} \frac{\dot{C}(h,A,B,t(h))}{\dot{C}(h,A,B,t(h)) + \dot{C}(h,A,0,t,(h)) + \dot{C}(h,0,B,t(h))}$$

$$= \prod_{h=1}^{n} \frac{R(h,A,B,t(h))\theta(h,A,B,t(h))}{R(h,A,B,t(h))\theta(h,A,B,t(h)) + R(h,A,0,t(h))\theta(h,A,0,t(h)) + R(h,0,B,t(h))\theta(h,0,B,t(h))}$$

$$L_2 = \prod_{j=1}^{m} \frac{\dot{C}(j,A,0,t(j))}{\dot{C}(j,A,B,t(j)) + \dot{C}(j,A,0,t(j)) + \dot{C}(j,0,B,t(j))}$$

$$= \prod_{j=1}^{n} \frac{R(j,A,0,t(j))\theta(j,A,0,t(j))}{R(j,A,B,t,(j))\theta(j,A,B,t(j)) + R(j,A,0,t(j))\theta(j,A,0,t(j)) + R(j,0,B,t(j))\theta(j,0,B,t(j))} \quad (3)$$

$$L_3 = \prod_{k=1}^{p} \frac{\dot{C}(k,0,B,t(k))}{\dot{C}(k,A,B,t(k)) + \dot{C}(k,A,0,t(k)) + \dot{C}(k,0,B,t(k))}$$

$$= \prod_{k=1}^{n} \frac{R(k,0,B,t(k))\theta(k,0,B,t(k))}{R(k,A,B,t(k))\theta(k,A,B,t(k)) + R(k,A,0,t(k))\theta(k,A,0,t(k)) + R(k,0,B,t(k))\theta(k,0,B,t(k))}$$

$$\theta(i,A,B,t(i)) = \rho(i,A)\rho(i,B)e^{\int_{t_0(i)}^{t(i)} [\lambda(i,A,s)+\lambda(i,B,s)]ds}$$

$$\theta(i,A,0,t(i)) = \rho(i,A)e^{\int_{t_0(i)}^{t(i)} \lambda(i,A,s)ds}\left[1-\rho(i,B)e^{\int_{t_0(i)}^{t(i)} \lambda(i,B,s)ds}\right]$$

$$\begin{cases} \theta(i,0,B,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\ \theta(i,0,0,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right], \end{cases} \quad (3)$$

continued

where $h, j,$ and k index fish recaptures with both tags retained, with tag A only, and with tag B only; n, m , and p are the total numbers of fish recaptures with both tags retained, with tag A only, and with tag B only.

In the estimation, we assumed that $t_0(i)=0$, there was no type-I tag shedding (i.e. $\rho(i,A)=\rho(i,B)=1$), and $R(i,A,B,t(i))=R(i,A,0,t(i))=R(i,0,B,t(i))$. The latter assumption makes Equation 3 independent of probability of reporting at time $t(i)$. We also set the instantaneous shedding rate of tag j (j=A,B) as a function of fish total length at release $L(i)$ and time at liberty $t(i)$ of the form $\lambda(i,j,t(i))=\beta_0(j)+\beta_1(j)L(i)+\beta_2(j)t(i)$, where $\beta_0(j)$, $\beta_1(j)$ and $\beta_2(j)$ are parameters to be estimated. Thus, $\lambda(i,j,t(i))$ has three terms and seven (2^3-1) nested models, since each term can be included or excluded in a nested model and a nested model has at least one term. Under these assumptions, Equation 3 becomes

$$L=L_1 \cdot L_2 \cdot L_3, \quad (4)$$

with

$$L_1 = \prod_{h=1}^{n} \frac{\theta(h,A,B,t(h))}{\theta(h,A,B,t(h))+\theta(h,A,0,t(h))+\theta(h,0,B,t(h))}$$

$$L_2 = \prod_{j-1}^{n} \frac{\theta(j,A,0,t(j)}{\theta(j,A,B,t(j))+\theta(j,A,0,t(j))+(\theta(j,0,B,t(j))}$$

$$L_3 = \prod_{k-1}^{n} \frac{\theta(k,0,B,t(k))}{\theta(k,A,B,t(k))+\theta(k,A,0,t(k))+\theta(k,0,B,t(k))}$$

$$\begin{cases} \theta(i,A,B,t(i)) = e^{[\beta_0(A)+\beta_1(A)L(i)+\beta_0(B)+\beta_1(B)L(i)]t(i) \quad \frac{1}{2}[\beta_2(A)+\beta_2(B)]t(i)^2} \\ \theta(i,A,0,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \\ \theta(i,0,B,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2} \\ \theta(i,0,0,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]\left[1-e^{[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \end{cases}$$

For the first experiment, $\lambda(i,A,t(i))=0$ because internal tags (tag A)were inserted into the shark's body cavity and were not shed, except under very unusual circumstances. For the same reason, although three recaptured school sharks appeared to have shed their internal tags (rows 9 and 21, Table 1), these events were actually due to failure to detect the tag upon recapture. Consequently, both tags were assumed to be present for these recaptures. Also, tag shedding rates of white and gray Petersen discs were estimated, singly or in combination, to examine their possible differences (Table 3). Data on $\lambda(i,A,t(i))$(Roto tags)

Table 3

Instantaneous rate of tag shedding for school shark estimated from data based on the first double-tagging experiment assuming that the shedding rates of internal tags (tag A) are zero, i.e., $\lambda(i,A,t(i))=\beta_0(A)=0$, and those of external tags (tag B) depend only on their types, i.e., $\lambda(i,B,t(i))=\beta_0(B)$; n is the number of recaptures. $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. J = J-tag; L = L-tag; S = S-tag; W = W-tag; G = G-tag. The word "and" indicates pooling of data: J and L for pooling data from J-tag and L-tag; M and F for pooling data from males and females. Estimates for tag A of J and L and tag B of G are the same as those for tag A of L and tag B of G; estimates for tag A of J and S and tag B of G are the same as those for tag A of S and tag B of G.

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	J	W	M and F	32	0.3718(0.1089)	9.4439
2	J	W	M	18	0.2829(0.1104)	5.4509
3	J	W	F	14	0.5816(0.2946)	3.3332
4	L	W	M and F	11	0.6446(0.3609)	2.3503
5	L	W	M	7	0.3617(0.2605)	1.3295
6	L	W	F	4	—	—
7	L	G	M and F	200	0.7347(0.1012)	45.4817
8	L	G	—	2	—	—
9	L	G	M	127	1.1439(0.2534)	14.3301
10	L	G	F	71	0.5202(0.1016)	27.4639
11	S	W	M and F	7	—	—
12	S	W	—	0	—	—
13	S	W	M	2	—	—
14	S	W	F	5	—	—
15	S	G	M and F	167	3.0653(0.4739)	47.9105
16	S	G	—	2	1.2692(1.5899)	0.3407
17	S	G	M	86	4.5992(1.0705)	18.1029
18	S	G	F	79	2.3509(0.4955)	26.9553
19	L	W and G	M and F	211	0.7291(0.0974)	47.8580
20	L	W and G	—	2	—	—
21	L	W and G	M	134	1.0272(0.2119)	16.8622
22	L	W and G	F	75	0.5466(0.1040)	28.3971
23	S	W and G	M and F	174	3.0857(0.4735)	48.0298
24	S	W and G	—	2	1.2692(1.5899)	0.3407
25	S	W and G	M	88	4.5993(1.0702)	18.1029
26	S	W and G	F	84	2.3912(0.4975)	27.1604
27	J and L	W	M and F	43	0.4165(0.1084)	12.1642
28	J and L	W	M	25	0.2993(0.1016)	6.8258
29	J and L	W	F	18	0.7464(0.3367)	4.0018
30	J and L	W and G	M and F	243	0.6460(0.0780)	59.5387
31	J and L	W and G	—	2	—	—
32	J and L	W and G	M	152	0.7457(0.1255)	27.0143
33	J and L	W and G	F	89	0.5508(0.0979)	31.7369
34	J and S	W	M and F	39	0.4434(0.1207)	11.6709
35	J and S	W	—	0	—	—
36	J and S	W	M	20	0.3162(0.1168)	6.1176
37	J and S	W	F	19	0.7587(0.3557)	4.4422
38	J and S	W and G	M and F	206	1.6579(0.2133)	80.2783
39	J and S	W and G	—	2	1.2692(1.5899)	0.3407
40	J and S	W and G	M	106	1.5043(0.2682)	45.5600
41	J and S	W and G	F	98	1.8729(0.3550)	34.0001

continued

were too limited from the second experiment (Table 2) to estimate two or more parameters. We estimated $\beta_0(A)$ only, which can, however, be scaled to $\beta_1(A)$ or $\beta_2(A)$ given $L(i)$ and $t(i)$. For tag B (Petersen discs or dart tags), all seven nested models of $\lambda(i,B,t(i))$ were fitted, where possible, to data from each tagging experiment. The final and most parsimonious model was decided by the χ^2 statistic (Seber and Wild, 1989, p.196–197). All parameters were estimated by minimizing –log(L) by using the simplex algorithm by a FORTRAN 77 program (available on request).

Results

Maximization of Equation 4 for both sets of tagging data yielded estimates of shedding rate for various (independent) combinations of fish sex, tag type, and tag position, and their (asymptotic) standard errors (Tables 3 and 4). If a tag was retained in all recaptured fish, we assumed that its shedding rate was zero in order to estimate other parameters of the model. Because shedding rates must be nonnegative, the assumption of zero shedding rate will lead to an underestimate of the parameter concerned and introduce a positive bias into the estimates of other parameters. The extent of such bias could be assessed by simulation studies but is beyond the scope of this work.

Fish length at release or time at liberty, or both, entered certain final models for $\lambda(i,B,t(i))$, only when the number of fish recaptured was small. By contrast, whenever there were many fish recaptures (e.g. rows 14–15 and 20–21, Table 1), neither factor entered the final model. Therefore, we conclude that fish length at release or time at liberty, or both, did not significantly affect tag shedding rates; and their inclusion in certain models was a result of too few recaptures.

Fish sex affected tag shedding rates of Petersen discs for some combinations of tag type and tag position. For a combination of a 50-mm-long and 23-mm-wide internal tag (J-tag) with a white Petersen disc (external) tag (W-tag) (rows 1–3, Table 3), $\lambda(i,B,t(i))$=0.3718 (±0.1089)/yr if data are pooled for both sexes of school shark, with a –log-likelihood of 9.4439. For the sex-specific model, $\lambda(i,B,t(i))$=0.2829 (±0.1104)/yr for males; $\lambda(i,B,t(i))$=0.5816 (±0.2946)/yr for females, with a (male and female) combined –log-likelihood of 8.7841 (=5.4509+3.3332). The increase in value of the –log-likelihood function for an extra parameter is, in this case, negligible ($\chi^2_{1,0.2507}$=2×(9.4439–8.7841)=1.3196), suggesting no statistically significant differences in tag shedding rates between sexes for white Petersen discs.

Table 3 (continued)

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	–log(L)
42	L and S	W	M and F	18	0.9094(0.4251)	3.4541
43	L and S	W	—	0	—	—
44	L and S	W	M	9	0.4791(0.3116)	1.7664
45	L and S	W	F	9	—	—
46	L and S	G	M and F	367	1.2892(0.1331)	116.1464
47	L and S	G	—	4	1.2729(1.5769)	0.3409
48	L and S	G	M	213	2.1071(0.3520)	41.2981
49	L and S	G	F	150	0.9537(0.1327)	67.8985
50	L and S	W and G	M and F	385	1.2679(0.1274)	119.8703
51	L and S	W and G	—	4	1.2729(1.5769)	0.3409
52	L and S	W and G	M	222	1.8674(0.2992)	45.8682
53	L and S	W and G	F	159	0.9818(0.1336)	68.9822
54	J and L and S	W	M and F	50	0.4753(0.1168)	14.1985
55	J and L and S	W	—	0	—	—
56	J and L and S	W	M	27	0.3252(0.1063)	7.4610
57	J and L and S	W	F	23	0.8956(0.3763)	4.8981
58	J and L and S	G	M and F	367	1.2892(0.1331)	116.1464
59	J and L and S	G	—	4	1.2729(1.5769)	0.3409
60	J and L and S	G	M	213	2.1071(0.3520)	41.2981
61	J and L and S	G	F	150	0.9537(0.1327)	67.8985
62	J and L and S	W and G	M and F	417	1.0891(0.1026)	137.7412
63	J and L and S	W and G	—	4	1.2729(1.5769)	0.3409
64	J and L and S	W and G	M	240	1.2738(0.1761)	63.3863
65	J and L and S	W and G	F	173	0.9478(0.1251)	72.8067

Table 4

Instantaneous rate of tag shedding for gummy and school sharks estimated from data based on the second double-tagging experiment assuming that $\lambda(i,A,t(i))=\beta_0(A)$ and $\lambda(i,B,t(i))=\beta_0(B)$. Tagging position refers to tag B's position; n is the number of recaptures; $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. The word "and" indicates pooling of data: Jumbo and Roto for pooling data from Jumbo tag and Roto tag; M and F for pooling data from males and females.

Row	Species	Tag A	Tag B	Position of tag	Sex	n	$\beta_0(A)$ (SE)/yr	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	gummy	Jumbo	dart	fin	M and F	32	0.1912(0.1349)	0.3770(0.1886)	19.5193
2	gummy	Jumbo	dart	fin	M	13	0.2133(0.2125)	0.5642(0.3260)	10.98
3	gummy	Jumbo	dart	fin	F	19	0.1771(0.1770)	0.1890(0.1890)	8.0212
4	gummy	Jumbo	dart	muscle	M and F	84	—	0.9239(-)	67.5957
5	gummy	Jumbo	dart	muscle	M	41	—	0.8550(0.2021)	34.5527
6	gummy	Jumbo	dart	muscle	F	43	—	0.9902(-)	32.9376
7	gummy	Roto	dart	muscle	M and F	91	0.1304(0.0747)	1.0502(0.1712)	71.5838
8	gummy	Roto	dart	muscle	—	1	—	—	—
9	gummy	Roto	dart	muscle	M	37	0.1581(0.1110)	0.8183(0.2187)	31.8327
10	gummy	Roto	dart	muscle	F	53	0.0918(0.0913)	1.2111(0.2563)	37.1817
11	gummy	Jumbo	dart	fin and muscle	M and F	116	0.0569(0.0402)	0.8278(0.1243)	91.8731
12	gummy	Jumbo	dart	fin and muscle	M	54	0.0586(0.0584)	0.8042(0.1749)	47.2285
13	gummy	Jumbo	dart	fin and muscle	F	62	0.0555(0.0553)	0.8503(0.1766)	44.6251
14	gummy	Jumbo and Roto	dart	muscle	M and F	175	0.0641(0.0369)	0.9828(0.1121)	141.3449
15	gummy	Jumbo and Roto	dart	muscle	—	1	—	—	—
16	gummy	Jumbo and Roto	dart	muscle	M	78	0.0809(0.0570)	0.8379(0.1484)	67.8238
17	gummy	Jumbo and Roto	dart	muscle	F	96	0.0447(0.0446)	1.0948(0.1656)	70.9707
18	gummy	Jumbo and Roto	dart	fin and muscle	M and F	207	0.0857(0.0381)	0.9172(0.1012)	164.2892
19	gummy	Jumbo and Roto	dart	fin and muscle	—	1	—	—	—
20	gummy	Jumbo and Roto	dart	fin and muscle	M	91	0.1011(0.0580)	0.8083(0.1361)	79.4274
21	gummy	Jumbo and Roto	dart	fin and muscle	F	115	0.0692(0.0487)	0.9989(0.1474)	82.5257
22	school	Jumbo	dart	fin	M and F	18	0.0973(0.0972)	0.2646(0.1530)	11.0858
23	school	Jumbo	dart	fin	M	3	—	—	—
24	school	Jumbo	dart	fin	F	15	0.1104(0.1103)	0.2948(0.1706)	10.6735
25	school	Jumbo	dart	muscle	M and F	21	0.1041(0.1038)	0.4262(0.1917)	14.7690
26	school	Jumbo	dart	muscle	M	12	0.1727(0.1725)	0.3219(0.2282)	6.6030
27	school	Jumbo	dart	muscle	F	9	—	0.5484(0.3201)	7.3704
28	school	Roto	dart	muscle	M and F	9	—	0.7845(0.3967)	8.5426
29	school	Roto	dart	muscle	M	3	—	—	—
30	school	Roto	dart	muscle	F	6	—	1.6867(0.8865)	5.6360
31	school	Jumbo	dart	fin and muscle	M and F	39	0.1003(0.0708)	0.3466(0.1230)	26.0748
32	school	Jumbo	dart	fin and muscle	M	15	0.1421(0.1419)	0.2700(0.1912)	7.0831
33	school	Jumbo	dart	fin and muscle	F	24	0.0773(0.0772)	0.3831(0.1571)	18.7670
34	school	Jumbo and Roto	dart	muscle	M and F	30	0.0798(0.0796)	0.5339(0.1793)	24.0789
35	school	Jumbo and Roto	dart	muscle	M	15	0.1188(0.1188)	0.2263(0.1602)	7.5881
36	school	Jumbo and Roto	dart	muscle	F	15	—	0.8882(0.3425)	14.0341
37	school	Jumbo and Roto	dart	fin and muscle	M and F	48	0.0876(0.0619)	0.4254(0.1233)	35.8236
38	school	Jumbo and Roto	dart	fin and muscle	M	18	0.1038(0.1037)	0.1997(0.1414)	7.9368
39	school	Jumbo and Roto	dart	fin and muscle	F	30	0.0746(0.0745)	0.5510(0.1755)	26.7306

However, for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a gray Petersen disc (external) tag (G-tag) (rows 7–10, Table 3), $\lambda(i,B,t(i))$= 0.7347 (±0.1012)/yr if data are pooled for both sexes, with a –log-likelihood of 45.4817. For the sex-specific model, $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr for males; $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr for females, with a (male and female) combined –log-likelihood of 41.7940 (=14.3301+27.4639). The increase in value of the –log-likelihood function for an extra parameter is statistically significant ($\chi^2_{1,0.0066}=2\times(45.4817-41.7940)=7.3754$), suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Similarly, for a combination of a 35-mm-long and 10-mm-wide internal tag (S-tag) with a gray Petersen disc (external) tag (rows 15–18, Table 3), $\lambda(i,B,t(i))$=3.0653 (±0.4739)/yr if data are pooled for both sexes, with a –log-likelihood of 47.9105. For the sex-specific model, $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr for males; $\lambda(i,B,t(i))$= 2.3509 (±0.4955)/yr for females, with a (male and fe-

male) combined –log-likelihood of 45.0582 (=18.1029+ 26.9553). The increase in value of the –log-likelihood function for an extra parameter is, again, statistically significant ($\chi^2_{1,0.0169}$=2×(47.9105–45.0582)=5.7046), again suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Notice, in these cases, that tag shedding rates for males nearly doubled those for females. For the second tagging experiment, no differences in tag shedding rates were found among sexes for either species of shark (Table 4).

The shedding rate of Petersen discs for the school shark was very high. When combined with a 50-mm-long and 23-mm-wide internal tag (J-tag), white Petersen disc (W-tag) had a shedding rate of $\lambda(i,B,t(i))$=0.2829(±0.1104)/yr or $100\times(1-e^{-0.2829}) \approx$ 24.64%/yr for males, and $\lambda(i,B,t(i))$=0.5816(±0.2946)/yr or 44.10%/yr for females (rows 1–3, Table 3). When combined with a 50-mm-long and 22-mm-wide internal tag (L-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr or 68.14%/yr for males and $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr or 40.56%/yr for females (rows 7–10, Table 3). When combined with a 35-mm-long and 10-mm-wide internal tag (S-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr or 98.99%/yr for males and $\lambda(i,B,t(i))$=2.3509 (±0.4955)/yr or 90.47%/yr for females (rows 15–18, Table 3). Other combinations of tag type and tagging position for the first tagging experiment did not yield reliable (in accuracy and precision) estimates of tag shedding rate because of insufficient data.

For the second tagging experiment, tag shedding rates varied considerably for both species of sharks (rows 1–10 and 22–30, Table 4). However, dart tags had a higher shedding rate than either Roto or Jumbo tags. For example, for male gummy shark tagged in the fin, dart tags had an instantaneous shedding rate of 0.5642 (±0.3260)/yr and Jumbo tags 0.2133 (±0.2125)/yr (row 2, Table 4). For either gummy or school shark, the shedding rate of dart tags placed in the fin was about half that of dart tags placed in the muscle (rows 1–10 and 22–30, Table 4).

Discussion

We developed a simple tag shedding model (Equations 1–4) to account for the effects of time at liberty, sex, size, tag position, and other factors and used a special case to estimate the instantaneous shedding rates of Petersen discs, Roto tags, and dart tags in two species of sharks. It can be used to estimate the shedding rates of two tags, singly or in combination, and has two interesting features. In Equation 1, both $F(i,t(i))$ and $M(i,t(i))$ are independent of the 16 state variables. This independence ensures that $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ are all expressible as a product (Equation 2), which in turn ensures that terms involving $F(i,t(i))$ and $M(i,t(i))$ in the likelihood function (Equation 3 or 4) are cancelled out. Thus, as in Xiao (1996a), our tag shedding model applies, even when $F(i,t(i))$ and $M(i,t(i))$ are arbitrary functions of time $t(i)$. On the other hand, if fishing and natural mortalities depend on the state variables of tags A and B, then terms in $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ involving four fishing mortalities $F(i,A,B,t(i))$, $F(i,A,0,t(i))$, $F(i,0,B,t(i))$ and $F(i,0,0,t(i))$ and four natural mortalities $M(i,A,B,t(i))$, $M(i,A,0,t(i))$, $M(i,0,B,t(i))$ and $M(i,0,0,t(i))$ cannot be factored out. Then, for estimation of parameters by maximizing Equation 3, particular functional forms of all the eight mortalities must be hypothesized. This tag shedding model is more general but more data-demanding. The other interesting feature of our tag shedding model is that Equation 3 is independent of probabilities of reporting $R(i,A,B,t(i))$, $R(i,A,0,t(i))$, $R(i,0,B,t(i))$ and $R(i,0,0,t(i))$ if these probabilities are identical, arbitrary functions of time $t(i)$ because of the way they enter Equation 3.

Statistically significant differences in shedding rates of Petersen discs between male and female school sharks were detected when many fish were recaptured. We do not know why such differences existed but we postulate that male sharks have a higher tag shedding rate because they are more active and would tend to rub off the tags and that female sharks have a lower tag shedding rate because they are larger and have thicker fins. An external fin tag, such as a Petersen disc, is shed only after its pin or locking mechanism has cut through the fin. The larger the tagged fish, the thicker is its fin and hence the farther the distance its pin or locking mechanism has to cut through to the posterior edge of the fin. Consequently, larger animals have lower shedding rates. Thus, sex is confounded in its effects with size. That is probably why the length at release of school sharks did not affect the shedding rates of Petersen discs within a wide size range examined, although the loss of anchor tags (Floy tags) was size-dependent for striped bass *Morone saxatilis* (Waldman et al., 1990) but size-independent for lake trout *Salvelinus namaycush* (Fabrizio et al., 1996). We could not detect differences between sexes with fewer recaptures, however, because the use of Equation 1 or 2 to resolve sexual differences in tag shedding rate requires many recaptures (see below).

Shedding rates of Petersen discs, Roto tags, and dart tags did not change with time at liberty. Some

tagged fish have higher shedding rates than others, because tags that are less securely attached are shed earlier. The proportion of less securely attached tags decreases with increasing time at liberty. This will yield an apparent decrease in tag shedding rate with time at liberty. A similar argument applies when tag shedding rates vary among individuals. The lack of a trend may indicate negligible tag losses from improper attachment, insignificant individual variability in tag shedding rate, or insufficient data (see below).

Estimates of tag shedding rates in Tables 3 and 4 must be used cautiously because only those that are based on many recaptures are reliable, whereas those that are based on few recaptures are unreliable. For example, the estimates of tag shedding rates for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a white Petersen disc (W-tag, external) (rows 4–6, Table 3) were based on only 11 recaptures (rows 11 and 12, Table 1), only one of which had retained both tags (row 11, Table 1), and hence are unreliable. No estimates could even be obtained for a combination of a 35-mm-long and 10-mm-wide (S-tag) internal tag with a white Petersen disc (W-tag, external) (rows 11–14, Table 3), despite seven recaptures, none of which had retained both tags (rows 16–18, Table 1). Similarly, no estimates could be obtained, for any tag combinations, from data on gummy sharks from the first double-tagging experiment, despite 20 recaptures, none of which had retained both tags (rows 1–8, Table 1). Equally unreliable estimates of tag shedding rates could also result from pooling of information while ignoring differences in its sources. For example, estimates from pooling all three internal tags (i.e. J-tag, L-tag and S-tag) (rows 54–65, Table 3) should be treated cautiously because of sexual differences inferred above. By contrast, for both sexes of school sharks, the estimates of shedding rates of gray Petersen discs are reliable for its combination with a 50-mm-long and 22-mm-wide internal tag (L-tag) (rows 9 and 10, Table 3) or with a 35-mm-long and 10-mm-wide (S-tag) internal tag (rows 17 and 18, Table 3) because information from many fish recaptures was used in their estimation. Much less reliable estimates were obtained for dart tags on gummy sharks (rows 5, 6, 9, and 10, Table 4). Although rather high in all cases, all these shedding rates are actually underestimated, as will be shown and published elsewhere.

Although we have examined only the effects of tag type, sex, length at release, and time at liberty on tag shedding, many other factors, such as tagging operator (Hampton, 1996), can also affect tag shedding rate. However, hundreds or even thousands of fish need to be recaptured (many more need to be released) to estimate effects of tagging operators reliably. Such a great demand of data is well expected of Equation 1 or 2, which is a compartmental model. The solution of a compartmental model can be given by a linear combination of exponentials and is known to yield bad ill-conditioning (Seber and Wild, 1989, p. 118–119). Indeed, for some compartmental models, no amount of data is sufficient for identifying model parameters. Similarly, the "best" model of all possible models of a general model is identifiable only by a sufficient volume of data. As mentioned above, fish length at release or time at liberty, or both, entered certain "best" models for $\lambda(i,B,t(i))$, when the number of fish recaptured was small, but did not, when there were many fish recaptures. This finding suggests that fewer data than sufficient cannot identify the "best" model. To detect and address problems with parameter and model identifiability for a particular general model (e.g. Equation 1 or 2), one might generate as large a set of data as necessary, for example, by duplicating each record of an existing set of data from a double-tagging experiment a necessary number of times, analyse it, and design one's tagging experiment accordingly (e.g. to determine the number of fish to be released and the expected number of fish to be recaptured).

Results of our study have major implications for future double-tagging experiments for estimating instantaneous tag shedding rate and for analysis of tagging data. Because estimation of a single parameter requires many fish recaptures and hence incurs considerable financial resources, use of an easily detected and permanent tag eliminates a need for considering tag loss and is preferred in any tagging experiment. However, with a commercially or recreationally harvested species, problems of tag reporting remain. Use of two readily detectable, identical tags with a moderate shedding rate in a double-tagging experiment reduces the number of parameters to be estimated by one half. A moderate shedding rate is necessary because too low a shedding rate requires some recaptures after a long time at liberty for reliable estimation of parameters; too high a shedding rate renders the tag useless for some applications.

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Areas, depths, and times of high discard rates of scup, *Stenotomus chrysops*, during demersal fish trawling off the northeastern United States

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In the waters off the northeastern United States, many stocks of commercial and recreational species have declined in recent years (Anthony, 1993; Sissenwine and Rosenberg, 1994; Collins, 1995; Matthiessen, 1995; NEFSC, 1995). Although much of the blame for these declines is ascribed to sustained overfishing, there also has been substantial concern over bycatch and discarding practices in key fisheries of the region, especially those involving demersal trawling (Murawski, 1994; Howell and Langan, 1987, 1992; Cadrin et al., 1995; Kennelly et al., 1997).

For many years scup (or porgy, *Stenotomus chrysops*) has been an important commercial species in the mid-Atlantic and southern New England regions, caught principally by otter trawling and to a lesser extent by pound nets, floating trap nets, and fish traps (Shepherd and Terceiro, 1994). Like many other key species in the region, annual commercial landings of this species have declined markedly in recent years from between 18,000 and 27,000 metric tons (t) in the 1950s and 60s to 6000 t in 1992 and 4400 t in 1993 (NEFSC, 1995). There is also an important recreational fishery for scup in this region, and recreational landings in recent years have accounted for 20 to 50% of the total annual catch. These have also declined from an estimated 3,100 t in the 1980s to 2100 t in 1992 and 1300 t in 1993 (NEFSC, 1995). Scientists at the 1995 Northeast Regional Stock Assessment Workshop for the scup stock in this region concluded that 1) it is currently overexploited; 2) it is at a low level of biomass; and 3) current high rates of exploitation of age 0–2 fish should be decreased as much as possible (NEFSC[1]).

As predicted by Wilk and Brown (1980) some time ago, one of the causes of mortality for young scup in this region is thought to be the incidental bycatch and subsequent discarding of this species from demersal trawlers that target other species, particularly squid (*Loligo* spp.). McKiernan and Pierce's[2] study of the inshore squid fishery in Nantucket and Vineyard Sounds, Massachusetts, showed significant discard of scup but, like Cadrin et al. (1995), they concluded that the inshore abundances of this species were more probably related to trawl effort throughout the region than to the relatively small effort of inshore squid trawlers. They concluded that significant numbers of small scup may be discarded by squid trawlers farther offshore where scup are known to migrate in the autumn (see also Finkelstein, 1971; Eklund and Targett, 1990) and recommended an examination of the discarding practices of these trawlers.

The most reliable way to quantify discards in commercial fisheries is for observers to record data during normal fishing operations (e.g. Jean, 1963; Powles, 1969; Young and Romero, 1979; Atkinson, 1984; Murawski et al., 1995). Information from such programs is a necessary prerequisite for the two main management alternatives used to reduce discards: 1) spatial and temporal closures to fishing in areas and times of high rates of discard of key species (i.e. discard "hotspots") (Murawski, 1992; Hendrickson and Griffin, 1993; Alverson et al., 1994, Kennelly, 1997); and 2) modifications to fishing gears and practices that improve selectivity (Robertson and Stewart, 1988; Isaksen et al., 1992; Hall, 1994; Broadhurst et al., 1996; Broadhurst and Kennelly, 1997).

Since 1989, the National Marine Fisheries Service's Northeast Fisheries Science Center (NEFSC) has operated a large-scale observer program in many of the fisheries off the northeastern United States from Maine to North Carolina (Murawski et al., 1995; Kennelly et al., 1997). The data collected from demersal trawlers in this program have provided an opportunity to examine the spatial and temporal occurrences of discarded scup in the offshore mid-Atlantic and southern New England trawl fishery.

[1] NEFSC (Northeast Fisheries Science Center). 1995. Report of the 19th northeast regional stock assessment workshop–the plenary. NOAA/NMFS/NEFSC, Woods Hole, MA. NEFSC Ref Doc. 95-09, 57 p.

[2] McKiernan, D. J., and D. E. Pierce. 1995. *Loligo* squid fishery in Nantucket and Vineyard Sounds. Massachusetts Div. Fish. Publ. 17648-75-200-1/95-3.47-CR, 62 p.

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Materials and methods

Field sampling

Each month between July 1990 and June 1994, Manomet Center for Conservation Sciences (under contract to the NEFSC) placed observers on board demersal trawlers working throughout the northeastern United States. The selection of vessels and trips undertaken did not adhere to any consistent survey design but was based on changing national, management and stock assessment priorities (Murawski et al., 1995) in addition to varying concentrations of fishing fleets in particular areas and times. As a consequence, the observer coverage of these trawlers was highly uneven throughout the period; some areas and times received high sampling and others received very little or no sampling. Of relevance to this paper are the observer data gathered in the southern New England and mid-Atlantic areas shown in Figure 1.

During observed trips, the contents of the codend from each tow were emptied onto the deck and sorted by the crew. If the entire catch could not be sampled, data were collected from a representative subsample. The data collected from each tow that were of relevance to this paper were the following: area, depth, date, time and tow duration, the weights of retained and discarded individuals of various species in the catch, the number of species caught, and the total weights of all species retained or discarded. Because of various operational and logistic reasons, not all tows from all trips were sampled for the weights of retained and discarded species; however, the data examined in this paper include only those tows that were completely sampled.

Analysis of data

Because of the lack of a consistent survey design in this observer program, the data generated could not be regarded as randomly collected, independent samples of the trawling effort of the region, and thus violated the basic assumptions required for conventional statistical analyses (see also Kennelly et al., 1997). Nevertheless, because of the size of the data set and its extensive spatial and temporal coverage, large subsets of data could be extracted for many areas and months and therefore permitted the identification of certain key areas, depths, and times of consistently high rates of scup discard (see "Results" section). The first and broadest examination of the data was to plot the discard rates for scup for all the areas sampled in the region to identify those areas that experienced consistently high rates. Next, discard rates for scup from each sampled tow in each of these identified areas was plotted against depth to

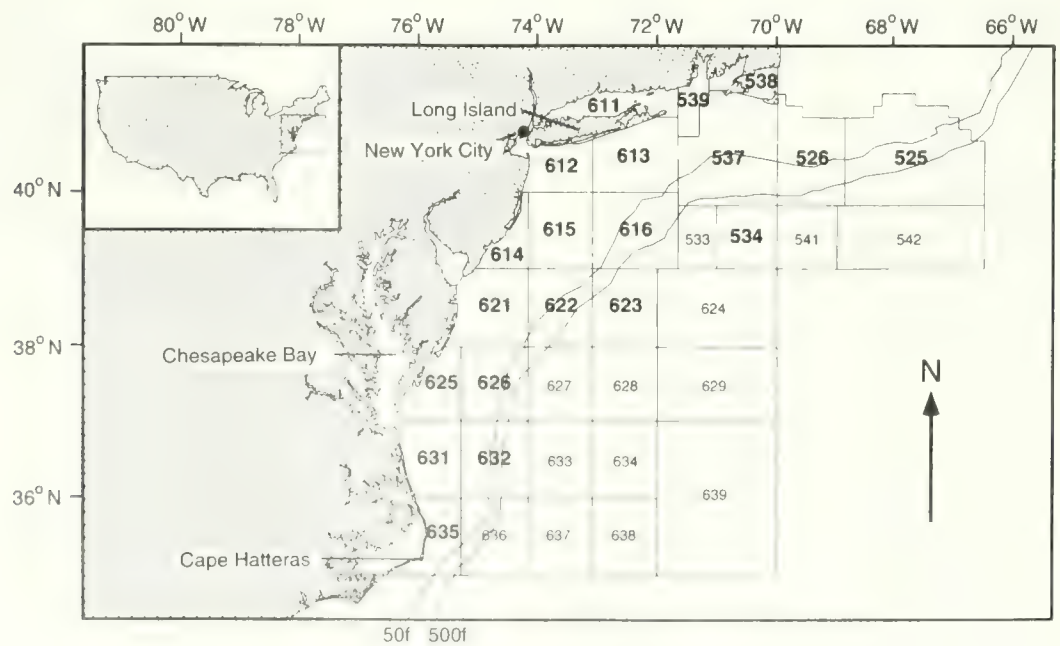

Figure 1

Map showing the various NMFS statistical areas examined in the present paper. Areas labelled in bold are those with sufficient observer coverage to be examined in Figure 2.

determine which depths yielded consistently high rates. Once these depths were identified, the discard rates of scup in these tows were plotted against time to determine the particular months when the high discards occurred. In this way, the large observer data set for the region was focussed to identify the particular areas, depths, and months that yielded high discard rates for scup. Finally, catches of other common species in these identified areas and times were examined by plotting their retention and discard rates.

Results

Figure 2 shows the average discard rates for scup (in pounds per hour towed) for the areas defined in Figure 1. All areas other than 526, 537, 539, 613, 615, 616, 621, 622, and 623 showed low discard rates for scup (defined as a maximum rate of less than 20 lb/h) or low levels of observer coverage (defined as less than 10 observed tows during the study), or both.

Figure 3 shows discard rates for scup against the depth of the tows sampled in each of the areas identified in Figure 2 above. Most areas recorded high discard rates across a range of depths, except areas 613 and 621 which showed marked concentrations from 30–40 fathoms (fm) and 6–17 fm respectively.

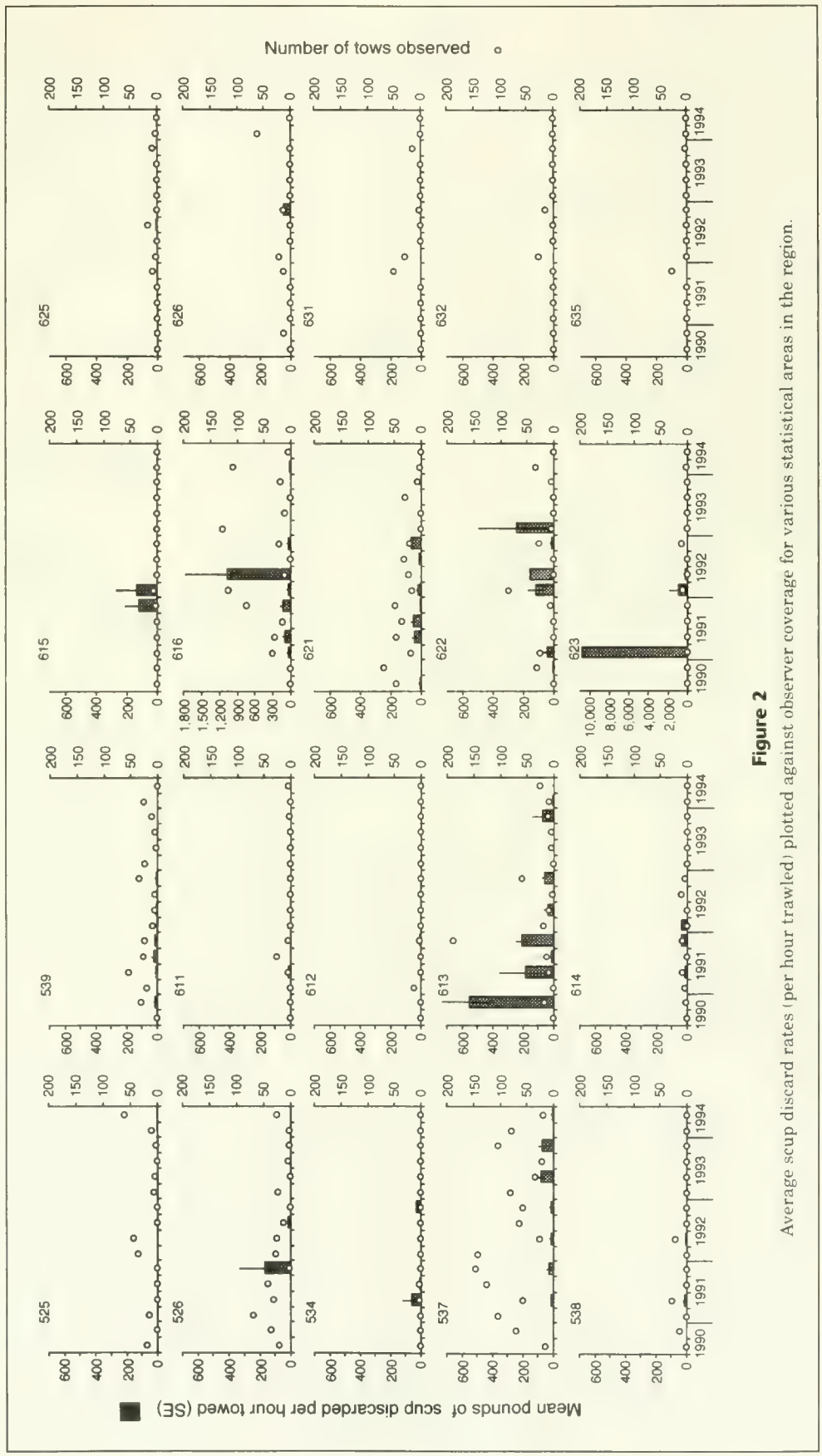

Figure 2
Average scup discard rates (per hour trawled) plotted against observer coverage for various statistical areas in the region.

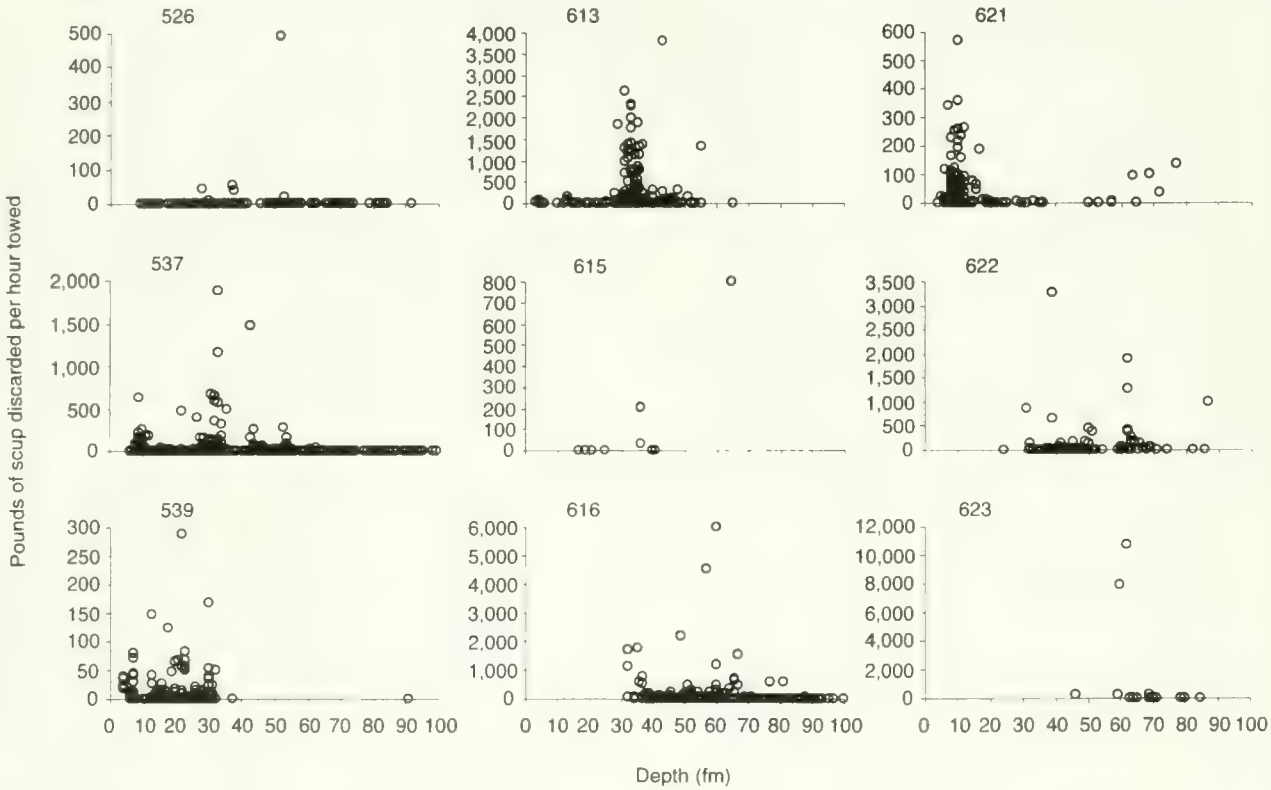

Figure 3

Scup discard rates (per hour trawled) plotted against depth for those areas in Figure 2 that showed consistently high rates of scup discard.

Figure 4 shows the timing of discard rates for scup in area 613 between 30 and 40 fm and in area 621 between 6 and 17 fm. For area 613, the highest rates at those depths occurred in November and December of each of the four years studied. Such a persistent trend for high scup discards was not evident for area 621, where highest rates occurred in May, August, and September 1991, and in September and October 1992.

Figure 5 shows the mean number of pounds retained and discarded for the most common species caught in all tows sampled in area 613, between 30 and 40 fm, in the months of November and December each year. Because of inconsistent identifications, data for squid and skates include data for all such species. Squid were by far the main retained species with an average of 507 lb/h. Scup and whiting, *Merluccius bilinearis,* were also retained in significant quantities at 227 and 223 lb/h respectively. The main discarded species was dogfish, *Squalus acanthias,* (672 lb/h), followed by scup (319 lb/h) and skates (236 lb/h), and lesser quantities of butterfish, *Peprilus triacanthus,* (96 lb/h), whiting (72 lb/h), and red hake, *Urophycis chuss,* (51 lb/h).

Discussion

The above treatment of a four-year subset of the NMFS sea sampling database indicated that trawling in a particular area (area 613), depth (30–40 fm), and time of year (November to December), consistently led to high discard rates for scup. Before discussing this result, however, it is necessary to consider the problems inherent in the data analyzed. In particular, the design of this observer program involved a nonrandom, nonindependent allocation of sampling effort that was uneven in space and time (see Fig. 2). These problems precluded 1) the use of conventional statistical analyses to detect trends and 2) the identification of patterns for all areas for all months. For example, the uneven observer coverage may have resulted in the identification of only 9 of the 20 statistical areas in the region as having high discard rates for scup (Fig. 2). Although adequate observer coverage seemed to occur across most of the depths in many of these nine areas (Fig. 3), not all areas had all depths sampled, precluding the conclusion that other depth-related areas of high scup

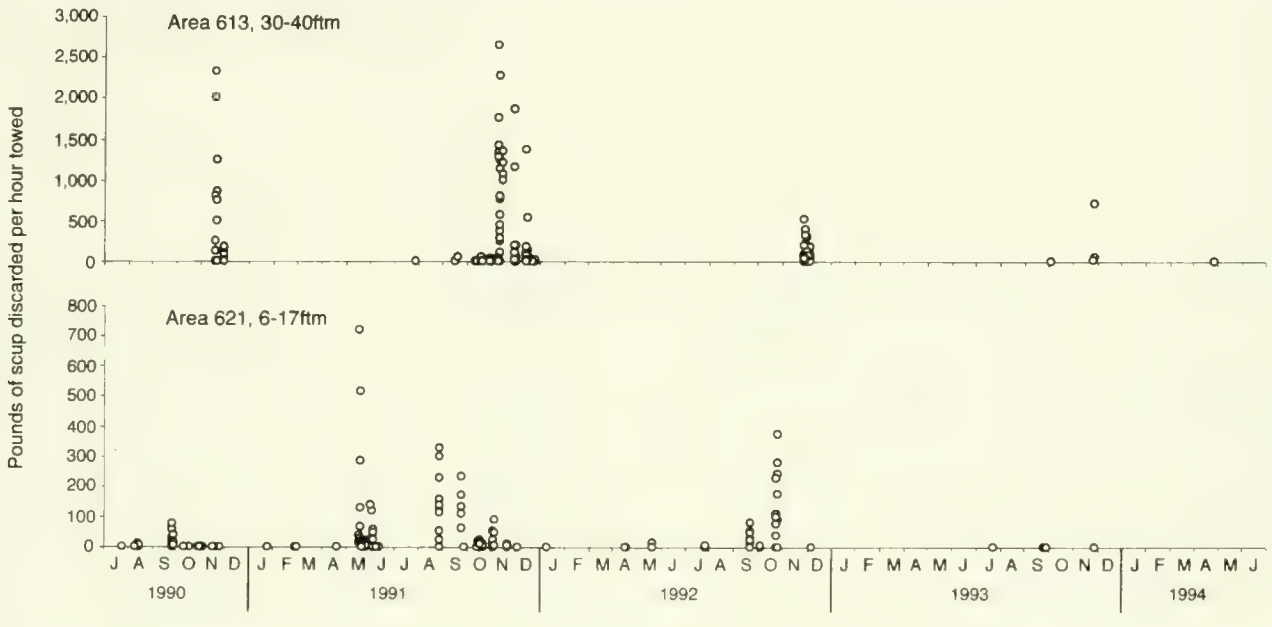

Figure 4

Scup discard rates (per hour trawled) plotted against time for those depths and areas in Figure 3 that showed consistently high rates for scup discard.

discard did not exist in the region (i.e. in addition to the identified depths in areas 613 and 621). Figure 4 shows the temporal pattern of scup discard in those areas and depths identified from Figures 2 and 3 and reveals a consistent pattern of high discard for area 613 but not for area 621. However, more observer coverage throughout the year could have provided evidence of other consistent peaks of scup discard in one or more areas and depths, or could have defined better the small period of high scup discard in area 613. For example, the data indicated that November and December were key months, but more sampling in October and January could have widened this time frame.

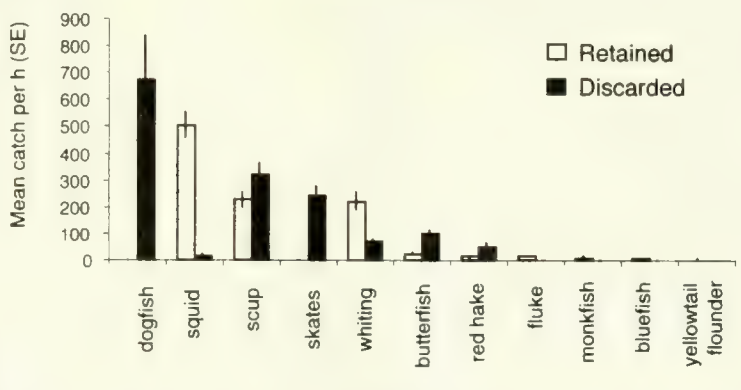

Figure 5

Retained and discard rates (per hour trawled) of the main species caught in those tows done in area 613, between 30 and 40 fm, in the months of November and December (the identified area and time of consistently high rates for scup discard).

A second problem with the data is that they were collected from many different boats, with different nets, horse powers, tow durations, etc. Although such problems are avoided in fishery-independent surveys by using standardized gears and sampling protocols, they are unavoidable when dealing with observer programs whose objective is to survey normal fishing operations across a variety of vessels, gear-types, etc. in order to detect fleet-wide patterns. Variation in observer data is inherent in all such programs, and it is only by doing properly designed and replicated, stratified, randomized observer surveys that such problems can be accounted for.

In most studies that have quantified bycatches, species-specific spatial, and temporal variabilities in

discarding often preclude the identification of definite areas and times of persistently high discards of species (see also Robin, 1991; Martinez et al., 1993; Liggins and Kennelly, 1996; Kennelly et al., 1997). The present study shows that high discard rates for scup were rarely consistent in particular areas and times, although one area and time did show some persistence throughout the four years: the relatively small area (area 613) off Long Island, New York, between 30 and 40 fm in the months of November and December each year. It is well known that from May to August each year scup spawn in estuaries, bays, and inshore areas south of Cape Cod (e.g. see Wilk and Brown, 1980; Eklund and Targett, 1990), particularly around Long Island (Finkelstein, 1971). In autumn, after spawning, they migrate south at greater depths towards their wintering grounds from southern New Jersey to Cape Hatteras, returning back to their inshore spawning grounds in spring (see Neville and Talbot, 1964; Wilk and Brown, 1980; Jeffries and Terceiro, 1985; Eklund and Targett, 1990). It is apparent from this behavior, that the occurrence of large numbers of scup as trawl discards in area 613 off Long Island in the autumn of each year coincides with their migration from Long Island's inshore waters to their wintering grounds farther south.

When spatial and temporal patterns in observer data reveal persistent areas and times of high discard rates, they can be used by fisheries managers to identify where and when various management tools can be applied to reduce discards. These tools usually involve either spatial or temporal closures to fishing (or both) or modifications to fishing gears and practices that reduce discards.

If fisheries managers consider the area and time of high scup discard identified in this paper as a candidate for a closure, the data in Figure 5 provide some information on the consequences this may have on landings of squid and other species. In the identified area and time, an average of over 507 lb of squid were retained per hour towed, whereas an average 319 lb of scup were discarded per hour towed. The actual numbers of fish involved were not available but, because the discarded scup were those individuals considered too small to retain, discarded weights often represent more individual fish per pound than retained weights. One could expect, therefore, that closing this area at this time would protect significant numbers of small scup, thereby assisting the 1995 Northeast Regional Stock Assessment Workshop's recommendation to decrease their exploitation (NEFSC[1]). Larger quantities of dogfish and lesser quantities of skates, butterfish, and whiting would also be protected by such a closure. The "cost" of such a closure, however, would be significant reductions in the landings of squid from the area at that time and lesser reductions in the landings of scup and whiting. One way of estimating the potential effects that such a closure strategy might have for the region is to compare the overall squid retained and scup discard rates with rates adjusted by excluding all tows done in the identified area and time. Throughout the region, the overall discard rate for scup during the four years was 37.5 lb/h (standard error (SE)=4.7), but if the tows done in the identified area and time are excluded, the overall rate falls to 27.3 lb/h (SE=4.5): a decrease of 27%. This should be compared to the overall retained rate of squid in the region of 128.5 lb/h (SE=6.1) falling to 114.9 lb/h (SE=6.0) if the tows done in the identified area and time are excluded —a decrease of 10.6%. It is important to note, however, that closing the area at this time to trawling will not simply remove trawling effort from the region but merely redirect it to other areas that may yield lower scup discards. This means that the effects on landings and discards in the region will not simply be those protected inside the closure but will be tempered by increased landings and discards outside the closure by the redirected vessels.

The other suite of management tools available to reduce discards in areas and at times of high discarding involve modifying fishing gears and practices to improve selectivity. Such modifications as the Nordmore Grid and square-mesh panels have proven successful in reducing discards of small fish in trawl fisheries (e.g. Carr, 1989; Isaksen et al., 1992; Broadhurst et al., 1996; Broadhurst and Kennelly, 1997), and modifications like downward sorting grids and horizontal panels in nets have reduced the bycatches of unwanted sizes of species in groundfish trawls (see Larsen and Isaksen, 1993; Engas and West[3]). For the issue of scup discarding in the northeastern United States, gear modifications would be a better management alternative than the closure strategy outlined above if they could reduce greater quantities of scup discards (and concomitantly reduce landings of squid and other species by smaller amounts) than those under a closure strategy. Such a general, gear-based solution is also advantageous because its adoption throughout the region would not only lead to reductions in scup discard in identified "hotspots" but in all areas where scup discarding occurs. The information provided in the present study identifies the ideal locations and times for any gear-based research that aims to reduce scup discard by trawlers and where and when any gear modifications

[3] Engas, A., and C. W. West. 1995. Development of a species-selective trawl for demersal gadoid fisheries. Int. Coun. Explor. Sea Council Meeting (CM) 1995/B+G+H+J+K:1.

should be initially implemented. At the time of writing this paper, several such gear-based discard reduction programs are currently underway in the region.

Acknowledgments

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Effects of live-bait shrimp trawling on seagrass beds and fish bycatch in Tampa Bay, Florida

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The use of live shrimp for bait in recreational fishing has resulted in a controversial fishery for shrimp in Florida. In this fishery, night collections are conducted over seagrass beds with roller beam trawls to capture live shrimp, primarily pink shrimp, *Penaeus duorarum*. These shrimp are culled from the catch on sorting tables and placed in onboard aerated "live" wells. Beds of turtlegrass, *Thalassia testudinum*, a species that has highest growth rates and biomass during summer and lowest during the winter (Fonseca et al., 1996) are predominant areas for live-bait shrimp trawling (Tabb and Kenny, 1969). Because of their use in seagrass beds, roller trawls were designed to roll over the bottom to reduce gear penetration and debris collection. Because turtlegrass has an extensive root system, it is not likely to be uprooted by roller trawls, but the roller on the trawl has been noted to break off and collect old turtlegrass leaves (Woodburn et al. 1957). On the Gulf Coast of Florida, bait shrimp are generally collected from turtlegrass beds year-round, but most shrimp are taken October through February (Berkeley et al., 1985). Trawl and culling times for this fishery, including that of Tampa Bay, are typically short, 5–20 and 2–15 min, respectively, to reduce debris collection and both injury and mortality to shrimp. Although no data were collected, Berkeley et al. (1985) suggested that such trawling for shrimp may be destructive to seagrass beds and juvenile fishes, including spotted seatrout, *Cynoscion nebulosus*, snapper, *Lutjanus* spp., and pigfish, *Orthopristis chrysoptera*. However, the effects of this type of trawling on finfish bycatch mortality are unknown.

Numerous studies of fish bycatch mortality have used otter trawls. These include consideration of the effects otter trawling has on cod, *Gadus morhua*, and American plaice, *Hippoglossoides platessoides*, in the Gulf of St. Lawrence, Canada (Jean, 1963); on red snapper, *Lutjanus campechanus*, in the Gulf of Mexico (Gutherz and Pellegrin, 1988); and on bycatch in the Torres Strait, Australia (Wassenberg and Hill, 1989; Harris and Poiner, 1990; Hill and Wassenberg, 1990). In these studies fish mortality ranged from 10% (Jean, 1963) to 80% (Jean, 1963; Wassenberg and Hill, 1989), depending on culling times, animal size, and temperature. Trawl and culling times (30–60 minutes and 15–45 minutes, respectively) in these studies were typically longer than those used by the Florida live-bait shrimp fishery.

Our study objectives were 1) to determine effects of a roller beam trawl on turtlegrass biomass and morphometrics during intensive (up to 18 trawls over a turtlegrass bed), short-term (3-hour duration) use and 2) to examine the mortality of bycatch finfish following capture by a trawl.

Methods

Sampling was done in August and November 1990 in Tampa Bay, Florida (Fig. 1). A commercial bait shrimp boat towed two 3.38 m wide, 0.8 m high stainless steel roller beam trawls simultaneously, one

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from each side of the vessel. These consisted of a net attached to a stainless steel frame with a slotted roller along the entire lower portion of the frame. Stainless steel finger bars, 0.8 m long, were fastened vertically, 5 cm apart, along the front top of the frame to exclude seagrass and other debris (Berkeley et al., 1985). Each roller beam trawl weighed ~75 kg. Nets were constructed of 2.56-cm stretched mesh and had a 1.90-cm stretched mesh tail bag.

Turtlegrass

Nine trawl areas were selected in turtlegrass beds near Tarpon Key (Fig. 1). Each consisted of a marked 40-m × 3.38-m plot of continuous turtlegrass cover. Within each 40-m plot, a central 20-m × 3.38-m impact area was marked. During August, we sampled turtlegrass by removing cores of it within the impact area of each plot prior to trawling and after 1, 3, and 9 trawls. In November, new plots were marked and samples were collected prior to trawling and again after 9 and 18 trawls. Trawl levels were increased in November because preliminary analysis of the August data did not reveal a significant effect on turtlegrass at the maximum trawl level.

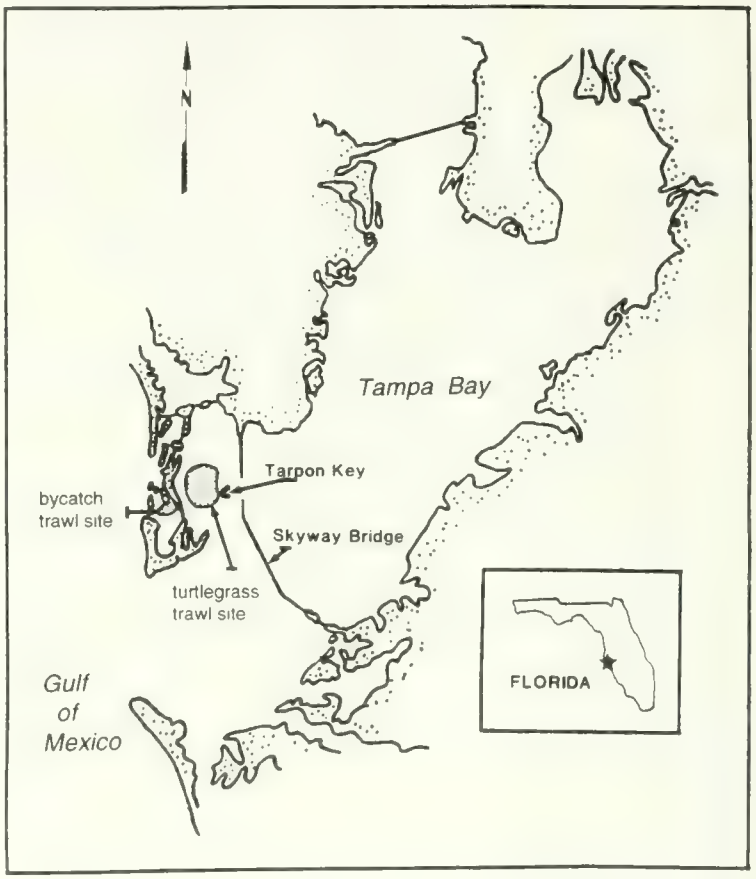

Figure 1

Location of bycatch and turtlegrass trawl sites within Tampa Bay, Florida, 27°40' North latitude, 82°27' West longitude.

Five 15-cm diameter × 20-cm deep substrate cores were taken randomly along a lengthwise midline transect within each impact area at each specified trawl level. For each core the shoot density, longest blade length, total blade length per shoot, and number of blades per shoot (from three randomly selected shoots) were recorded. The turtlegrass standing crop for each core was measured separately for above- and below-ground dry-weight biomass (dried at 60°C for at least 48 hours).

The sequential seagrass measurements within each replicate plot were used in regression analysis to detect rates of decrease for each of the different plant parameters as a function of trawl level. The regression slope (rate of decrease) for each plot was calculated for each plant parameter. Mean rate of decrease for each plant parameter was calculated for each month (all plots combined, n=9 for each month). T-tests were used to compare differences (P<0.05) in mean rate of decrease for each plant parameter for each month.

Mortality of bycatch fish

The bycatch collection site was southwest of Tierra Verde, near the mouth of Tampa Bay (Fig. 1). Each month 30 trawls of 5-min duration were made at this site over three consecutive nights. Trawl and culling times selected were based on observations of commercial live-bait shrimp fishing vessels and shortest times observed used to obtain conservative estimates of bycatch fish mortality. In August, the catch from one net of a trawl pair was allowed to sit on the culling table for 2 min prior to placement in the on-deck live well. The catch from the other trawl net was discarded. While the catch was sitting on the culling table, algae and detritus were removed to reduce subsequent fish entanglement. To reduce the effect of predation on mortality estimates, hardhead catfish, *Arius felis*, were removed from the catch. Bycatch for each trawl was placed in its own separate holding pen, which was held on deck inside an aerated 300-L live well until transferred to a final unvegetated holding site. Holding pens along with bycatch contents were transferred from the on-deck live well to the holding site in a 76-L seawater tank. On-deck holding times were 15 min, transport 5 min. Once at the holding site, pens were placed in the water at a low tide depth >1 m (the minimum) and anchored.

Holding pens were cubical, 1.25 m on each side, constructed of 6.4-mm mesh and had removable mesh tops. A 5-cm diameter polyvinylchloride collar was attached around the top sides of the pen to provide floatation. The mesh top and float collar prevented fish from escaping over the sides, and the top prevented avian predation. Lead-core line was sewn to the bottom seams of each pen to maintain pen volume. Loops attached to each corner of the pen enabled us to anchor the pens with conduit poles.

Owing to low abundance of fish bycatch in November, collection methods were modified; the bycatch from both of the paired trawl nets was combined (only a single trawl net was processed in August), and placed into a single holding pen. Handling procedures were also changed to estimate fish bycatch mortality more conservatively by eliminating catch culling time. In November the catch was placed directly into an aerated 76-L transport tank and during transport to the hold site, algae, detritus, and hardhead catfish were removed. Thus, bycatch mortality results for the two months were not directly comparable. In addition, during November the holding pens were deployed prior to bycatch collection, and the trawl catch was subsequently transferred from the 76-L transport tank into individual holding pens.

Pens were checked for dead fish (no opercular movement) following initial placement at the hold site, and then at intervals of 2, 8, 12, 24, and 36 hours. Checks involved inspecting each holding pen by systematically lifting portions of the pen netting so that the entire volume, net sides, and bottom could be visually inspected for dead fish while allowing surviving fish to remain immersed. Dead fish were collected at each time check and preserved in 10% formalin. At 36 hours, all dead and live fish were separated and preserved. Fish were identified, and standard length and body depth were measured (to the nearest 0.5 mm). The number of individuals and weights of each species (to the nearest 0.01 g) were recorded for each trawl and holding pen time check. Fish with a body depth <7.5 mm were excluded from survival measurements because they were able to escape through the mesh and would cause an unrepresentative mortality estimate.

Because the number of individuals per species per trawl was generally <5, we pooled all 30 trawls for each month to assess survival. The more numerous fish species (spotted seatrout, *Cynoscion nebulosus*, pinfish, *Lagodon rhomboides*, and silver perch, *Bairdiella chrysoura)* were subdivided into small (25.0–65.0 mm standard length, SL) and large (65.5–125.0 mm SL) size classes for mortality comparisons. Mojarra, *Eucinostomus* spp. (including silver jenny, *Eucinostomus gula*), were smaller and were subdivided into small (25.0–55.0 mm) and large (55.5–95.0 mm) size classes so that we could examine size-related mortality. Determination of differential size-class mortality was tested with log-linear model analysis ($P<0.05$).

Salinity and air and water temperatures were measured hourly during bycatch trawling.

Results

Turtlegrass

Regression analysis to estimate mean rate of decrease showed no significant ($P>0.05$) reduction in mean shoot density, number of blades per shoot, longest blade length per shoot, total blade length per shoot, or above- and below-ground biomass with increased trawling during either month. Monthly vegetation measurements at each trawl level (all nine sites combined) are shown in Table 1.

Fish bycatch

We collected a total of 5901 fish representing 42 species; 3262 fish (29 species) in August, 2639 fish (36 species) in November. Mojarra (including silver jenny) were 79.3% (August) and 52.1% (November) of the total catch (Table 2). Most mojarra were smaller than 40 mm SL and were identified as *Eucinostomus* spp., whereas all larger Gerreidae could be identified as silver jenny. The unreliability of the identification of smaller Gerreidae (those smaller than 40 mm SL) precluded their definitive identification to species (Matheson and McEachran, 1984). Mojarra less than 40 mm composed 60.0% (August) and 24.7% (November) of all fish collected, and silver jenny represented 19.3% (August) and 27.4% (November) of all fish collected (Table 2).

Survival was variable (0–100%) among species and months (Table 2; Fig. 2). Among the abundant species (those with at least 20 individuals for each month), high survival was observed for gulf toadfish, *Opsanus beta*, pigfish, pinfish, and gray snapper, (Table 2; Fig. 2). Abundant species with low survival were silver perch, mojarra, silver jenny, and spotted seatrout. Greatest mortality in most species occurred within the first 8 or 12 hours after collection (Fig. 2).

Small fish were significantly ($P<0.05$) more susceptible to trawl-induced mortality than larger fish (Table 3). This was particularly evident for silver perch, spotted seatrout, pinfish, and mojarra (including silver jenny).

Species-specific survival was greater in November than August (Table 2; Fig. 2). For those species for which at least 20 individuals were collected each

month, an average increase of 30.5% species-specific survival was observed in November compared with August. Silver perch (63.6%), gulf pipefish, *Syngnathus scovelli*, (48.1%), and gray snapper (35.0%) had the highest survival increases.

Average air and water temperatures observed were 31 and 32°C, respectively, in August, 23 and 24°C, respectively, in November. Salinity averaged 35 ppt during both months.

Discussion

Because roller trawls were designed to reduce seagrass fragment collection, it has been assumed that they have minimal impact on seagrass habitat (Tabb and Kenny, 1969; Berkeley et al., 1985). We were unable to detect significant trawl impacts on shoot density, structure, or biomass of turtlegrass by intensive short-term (18 trawls within three hours) trawling. This finding supports conjectures by Woodburn et al. (1957) and Tabb and Kenny (1969) that roller trawls have minimal impact on turtlegrass habitat.

However, we did not test for effects of repetitive trawling over turtlegrass beds over a longer period of time. Trawling may cause elevated localized turbidity, which could chronically reduce the potential for seagrass to perform photosynthesis (Kenworthy and Haunert, 1991). In contrast, limited trawling in areas with substantial epiphytic growth and numerous senescent turtlegrass leaves may enhance light availability by removing old plant parts (Woodburn

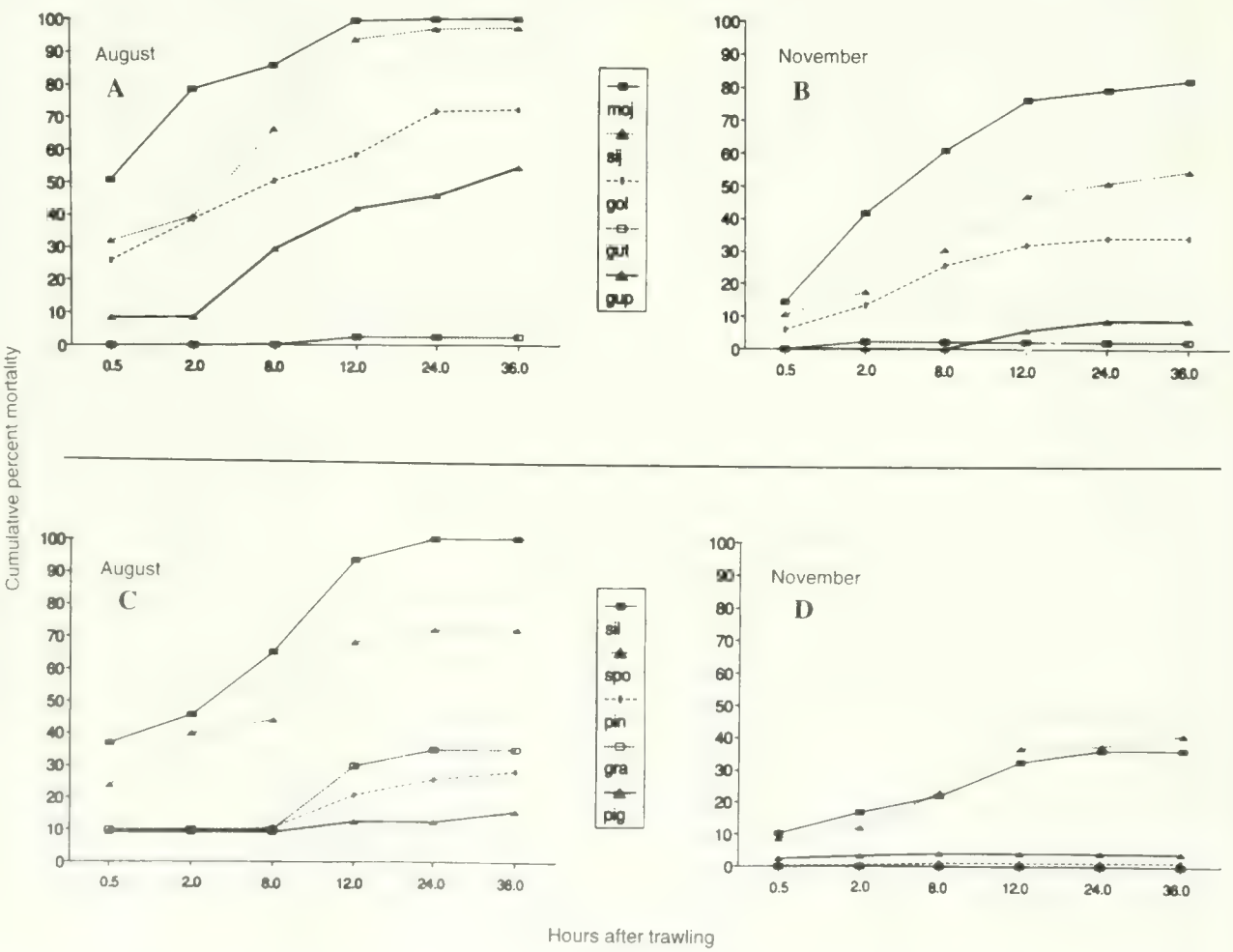

Figure 2

(**A–D**) Cumulative percent mortality in August and November of the abundant (at least 20 individuals per sample month) species collected with shrimp trawls and held in floating pens for 36 h. As noted in the text, handling procedures differed between the two collection periods. Species codes: moj = mojarra, sij = silver jenny, gol = goldspotted killifish, gut = gulf toadfish, gup = gulf pipefish, sil = silver perch, spo = spotted seatrout, pin = pinfish, gra = gray snapper, and pig = pigfish.

et al., 1957) and epiphytic growth from the plants (author's personal observation).

Trawling may affect associated faunal communities by collecting and redistributing macroalgae and turtlegrass litter. Redistribution can reduce the habitat complexity of one area and increase that of another. The alteration of habitat can in turn influence species composition and abundance (Gore et al., 1981; Kulczycki et al., 1981; Leber, 1985).

Fish species were not equally susceptible to mortality by exposure or net injury. Regardless of handling procedures, mojarra were highly susceptible to mortality. At the other extreme, oyster toadfish and striped burrfish, *Chilomycterus schoepfi*, were much less susceptible to trawl-induced mortality. Because of differential species mortality, fish species diversity and composition may be altered in areas of intense or long-term trawling.

Mortality and size were inversely related for numerous species, also noted by Jean (1963) for cod and American plaice, and by Fritz and Johnson (1987) for freshwater drum, *Aplodinotus grunniens*. A pos-

Table 1

Mean (±1 SE) shoot density, morphometrics, and biomass of turtlegrass per 176.7 cm^2 at selected trawl levels during August and November. For each trawl level during a month $n = 9$.

Number of trawls	Shoot density	Number of blades per shoot	Longest blade per shoot (cm)	Total length all blades per shoot (cm)	Above-ground biomass (g)	Below-ground biomass (g)
August						
0	8.1 (0.8)	2.5 (0.1)	31.6 (3.0)	63.5 (7.4)	1.3 (0.1)	7.4 (0.6)
1	7.1 (1.1)	2.4 (0.1)	32.4 (2.0)	61.3 (3.7)	2.3 (0.4)	7.0 (1.1)
3	7.8 (0.9)	2.4 (0.1)	34.0 (2.6)	64.4 (6.4)	2.2 (0.2)	7.2 (1.0)
9	9.1 (0.9)	2.4 (0.1)	28.3 (1.6)	55.2 (3.3)	1.5 (0.1)	8.3 (0.8)
November						
0	10.2 (0.7)	2.3 (0.1)	24.1 (1.2)	41.4 (2.7)	1.1 (0.1)	7.1 (0.6)
9	10.4 (0.4)	2.3 (0.1)	23.7 (0.9)	40.2 (2.0)	1.2 (0.1)	7.5 (0.5)
18	10.4 (0.6)	2.2 (0.1)	23.3 (1.4)	38.3 (2.3)	1.1 (0.1)	7.3 (0.6)

Table 2

Fish collected during August and November live-bait shrimp trawling in Tampa Bay, Florida. Percent survival was determined 36 hours after collection.

		Total number caught		Percent of total catch		Percent survival	
Common name	Scientific name	August	November	August	November	August	November
Mojarra (<40 mm)	*Eucinostomus* spp.	1956	655	60.0	24.7	0.5	18.2
Silver jenny	*Eucinostomus gula*	629	725	19.3	27.4	3.2	45.7
Goldspotted killifish	*Floridichthys carpio*	182	82	5.6	3.1	36.8	65.0
Pinfish	*Lagodon rhomboides*	152	259	4.7	9.8	71.7	98.1
Scaled sardine	*Harengula jaguana*	52	11	1.6	0.4	15.8	54.6
Silver perch	*Bairdiella chrysoura*	46	77	1.4	2.9	0.0	63.6
Rainwater killifish	*Lucania parva*	42	9	1.3	0.3	28.6	44.4
Gulf toadfish	*Opsanus beta*	40	101	1.2	3.8	97.5	98.0
Pigfish	*Orthopristis chrysoptera*	32	122	1.0	4.6	84.4	95.9
Spotted seatrout	*Cynoscion nebulosus*	25	117	0.8	4.4	28.0	59.0
Gulf pipefish	*Syngnathus scovelli*	22	33	0.7	1.2	45.8	93.9
Gray snapper	*Lutjanus griseus*	20	46	0.6	1.7	65.0	100.0
Striped burrfish	*Chilomycterus schoepfi*	13	198	0.4	7.5	100.0	99.5
Blackcheek tonguefish	*Symphurus plagiusa*	11	21	0.3	0.8	63.6	90.5
Planehead filefish	*Monacanthus hispidus*	1	84	<0.1	3.2	0.0	95.2
Southern puffer	*Sphoeroides nephelus*	0	26	0.0	1.0		96.2
Others		39	73	1.2	2.8	33.3	82.2

sible explanation for perceived differences in trawl-induced mortality between small and large size-class fish may be attributed to larger fish having a greater proportion of muscle tissue and larger energy stores than smaller fish; the larger fish are thus able to avoid net contact during prolonged trawl tows, (Fritz and Johnson, 1987). This may cause small fish to be more susceptible than large fish to stress and mortality due to capture. Consequently, high mortality of small individuals, directly or indirectly due to trawling, could potentially reduce the local stock of juvenile fish. This reduction in juvenile fish in turn could reduce the reproductive potential of a species and alter species diversity and composition within affected areas (Wassenberg and Hill, 1989).

Greater survival during November was most evident for silver perch, gulf pipefish, and gray snapper. However, we were not able to assess whether observed increased survival was the result of changes in handling procedures that we instituted (culling versus no culling), or to seasonal factors, such as differences in water temperature as noted by Jean (1963), between our survey months. The 2-min culling time and high August air temperature may have substantially stressed the fish in our study. Also, the higher water temperature in August may have reduced the ability of fish to recuperate from handling because of increased respiratory demand (Alderdice, 1963; Bond, 1979) and lower ambient dissolved oxygen levels (Raymont, 1980). However, even with the changes in handling instituted in November to reduce stress, net injury alone appeared to cause substantial mortality in mojarra, spotted seatrout, silver perch, and goldspotted killifish, *Floridichthys carpio*. Mean size of fish caught was larger in November than in August; this too may have contributed to the higher survival observed.

Fish abundance per holding pen was not recorded until the end of the 36-h mortality observation period. Because of this, and the fact that predation of live and dead individuals within the pens was not measured, the mortality for smaller species or smaller individuals of a species may be conservative. However, the initial confinement may have also enhanced the survival of injured or disoriented fish by reducing predation that might have been experienced in an open system. Even if bycatch organisms survive trawling and culling they may be quite susceptible to predation. High postrelease predation on bycatch has been observed by prawn trawlers (Hill and Wassenberg, 1990), and this fate probably awaits much of the bycatch overboarded during bait-shrimp trawling. Many bait-shrimp boat captains have reported schools of hardhead catfish following boats and feeding on the bycatch as it is thrown overboard. We similarly observed numerous hardhead catfish and other predatory fish following our boats and feeding on bycatch, and numerous such predatory individuals were collected during our sampling.

Trawl-induced mortality may occur past our 36-h observation period. Numerous fish still alive after the 36-h observation period had missing caudal fins or ulcers, or both. Such fish are were susceptible to subsequent mortality through predation or infection, or both. Moreover, individuals recaptured and culled again in heavily exploited areas could suffer high mortality rates because of cumulative stress. To understand better the effects of this fishery on the resident fauna, we need additional evaluation of the effects of temperature on mortality; the consequences of postrelease predation, delayed mortality due to initial sublethal damage, and subsequent infection; and finally an evaluation of the potential for recapture of bycatch fish.

Table 3

Percent fish mortality in relation to standard length (mm) for species with 20 or more individuals collected during each month. Parentheses indicate number of individuals in a size class. Asterisks (*) indicate significant differences $P<0.05$), based on log-linear model analysis, in mortality between size classes.

Species	Collection period	Size class (mm)	
		25.0–65.0	65.5–125.0
Silver perch	August	100.0 (42)	100.0 (4)
	November*	46.0 (50)	14.8 (27)
Spotted seatrout	August*	65.0 (20)	20.0 (5)
	November*	52.6 (78)	17.9 (39)
Pinfish	August*	47.1 (34)	22.9 (118)
	November		1.5 (259)
		25.0–55.0	55.5–95.0
Mojarra	August	99.1 (2435)	92.2 (153)
	November*	71.0 (1256)	28.0 (125)

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Distribution and relative abundance of sea turtles caught incidentally by the U.S. pelagic longline fleet in the western North Atlantic Ocean, 1992–1995

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The distribution and abundance of threatened and endangered species of sea turtles in offshore waters are not well understood. Early oceanographic flights designed to record sea surface temperatures along the Atlantic continental shelf by the U.S. Coast Guard illustrated that aerial surveys for large pelagic fish, marine mammals, and sea turtles were possible (Deaver[1]). Aerial surveys have since proven a cost-effective method of obtaining observational data on sea turtles and have helped researchers understand basic distributional patterns (Hoffman and Fritts, 1982; Fritts et al., 1983; Schroeder and Thompson, 1987; Shoop and Kenney, 1992). Additional sources of pelagic sea turtle data are fishery observer and vessel logbook programs. The U.S. Atlantic pelagic longline fishery for tuna, *Thunnus* spp., and swordfish, *Xiphias gladius*, incidentally captures threatened and endangered sea turtles, which have either ingested baited hooks or become entangled or hooked externally, or both. This paper examines the seasonal distribution and relative abundance of these turtles caught incidentally by the U.S. Atlantic pelagic longline fleet from 1992 through 1995.

[1] Deaver, J. W. 1975. Aerial oceanographic observations, July 1969–June 1970, Cape Cod, Massachusetts to Miami, Florida. U.S. Dep. Trans., Coast Guard Oceanogr. Unit, Oceanogr. Rep. CG 373-68, 27 p. [NTIS Accession No. AD-A014 415.]

Materials and methods

The fishery data used in this analysis are from the National Marine Fisheries Service (NMFS) pelagic logbook program managed by the Southeast Fisheries Science Center, Miami Laboratory. The logbook program was initiated in 1991 and requires U.S. Atlantic longline vessels to report daily catch and effort data. Specific longline information from the pelagic logbooks includes target species, type of bait, set and haulback dates and positions, length of mainline, number and lengths of gangions and floatlines, and numbers of light sticks and hooks set (Cramer, 1996). Sea turtle bycatch information was added to the logbook data form in 1992. Only sets targeting tuna or swordfish, or both, are analyzed here because the shark longline fishery is significantly different temporally, spatially, and geographically. NMFS logbook data for 1992–95 were analyzed by nine geographic fishing areas established by the NMFS Miami Laboratory (Fig. 1). Biological data of captured turtles were provided by NMFS observers placed aboard selected longline vessels (Lee et al., 1995; Gerrior, 1996). Sea turtle species identifications from the logbook data were edited to include only leatherback, *Dermochelys coriacea*, and loggerhead, *Caretta caretta*, sea turtles. This decision was based on the known distribution, abundance, and biology of sea turtles in the area, and the fact that some vessel captains and NMFS observers were unable to identify accurately all turtles encountered.

Results and discussion

The typical U.S. pelagic tuna and swordfish longline consists of a mainline, suspended horizontally by floats at a set depth, that has a series of baited hooks hanging vertically. The gears used for both target species are essentially the same. However, swordfish fishermen generally work at night using chemical light sticks suspended above the hooks to attract bait fish and tuna fishermen generally fish during the day without light sticks. Still, there are indications from logbook data that some of the longline fleet apparently target both tunas and swordfish and alter fishing strategies and gear configurations depending on the main target species, geographic location, and season (Hoey, 1983; Sakagawa et al., 1987). The U.S. pelagic longline fishery has evolved over the years from cumbersome New England style gears to lighter Florida style gears (Berkeley et al., 1981) and are significantly different from the gears used by the Japanese who targeted bluefin tuna in the western Atlantic (Lopez et al., 1979; Witzell, 1984). The gears currently in use on U.S. vessels vary considerably; they average about 47 km long and have 429 hooks suspended by 174 floats 54 m below the sur-

Manuscript accepted 24 April 1998.
Fish. Bull. 97:200–211 (1999).

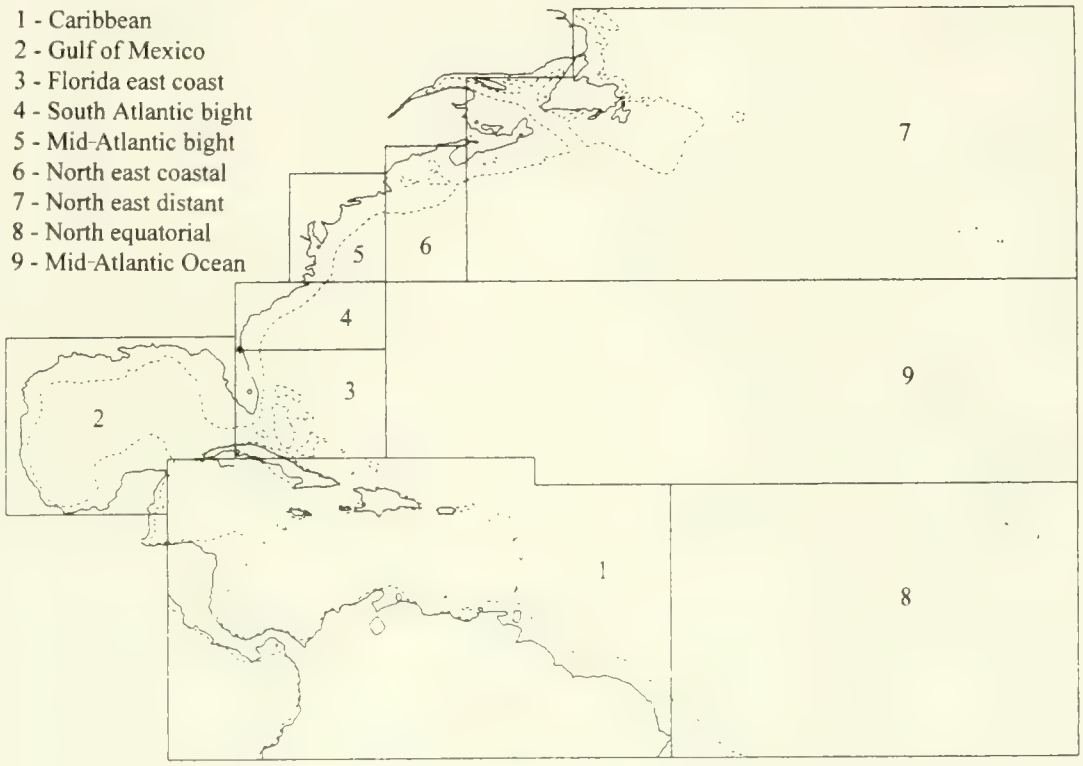


Figure 1

The NMFS pelagic fishing areas. Dashed line represents the 200-m isobath.

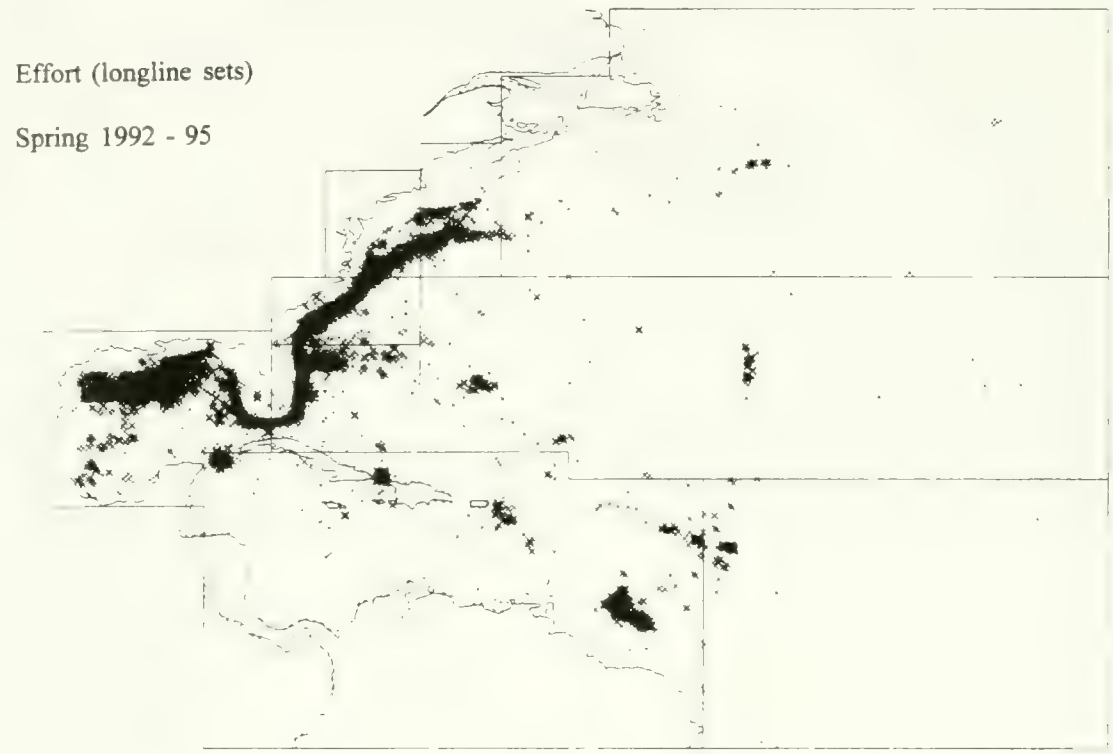
face (Power[2]). Pelagic longline fishing effort also changes temporally and spatially, depending on target species, season, and location (Fig. 2), although the overall effort for the entire area has not changed significantly over recent years (Cramer, 1996). Most effort is closely associated near the 200-m isobath along the edge of the continental shelf off the U.S. and off the shelf near the southeastern edge of the Grand Banks and often coincides with major current systems and thermally dynamic areas (Podesta et al., 1993). The most noticeable seasonal shift in fishing effort is the summer–fall swordfish fishery at the Grand Banks that moves to the Caribbean in the winter.

Leatherback sea turtles

A total of 1264 leatherback sea turtle captures were recorded in the NMFS pelagic logbooks for 1992–95 (Table 1). Total numbers of individual turtles caught are unknown because some turtles may have become entangled more than once. Year-round leatherback captures averaged 316 individuals per year (range: 198–452); June through November were the most important months with 1047 captures (82.7%). The mid-Atlantic, northeast coast, and northeast distant waters (areas 5–7) were the most productive, with 1035 (81.9%) combined captures. Of these, the northeast distant (area 7) accounted for 593 (46.8%) of the total leatherback turtle captures. Leatherback sea turtles are captured sporadically throughout the fishing area in the winter and spring seasons and become more abundant during the summer and fall, particularly in fishing areas 5–7 (Fig. 3). September was the most productive month with 278 (21.9%) captures for these areas combined. Reported catches varied annually (Table 2). Leatherback sea turtles were too large for observers to bring on deck for length and weight measurements, but the mean estimated carapace length of 110 individuals observed from the decks of northwest Atlantic fishing vessels was 160 cm.

Catch-per-unit-of-effort (CPUE) values indicated that loggerhead sea turtle capture rates varied considerably between areas (Table 3) but were highest

[2] Power, J. H. 1995. Analysis of the longline fishery effort, catch, and bycatch in the southwest Atlantic and Gulf of Mexico. U.S. Dep. Commer., Natl. Mar. Fish. Serv. Southeast Regional Office, 9721 Executive Center Drive, North, St. Petersburg, FL 33702. NOAA-NMFS-MARFIN Final Report, NA37FF0040-01, 96 p.



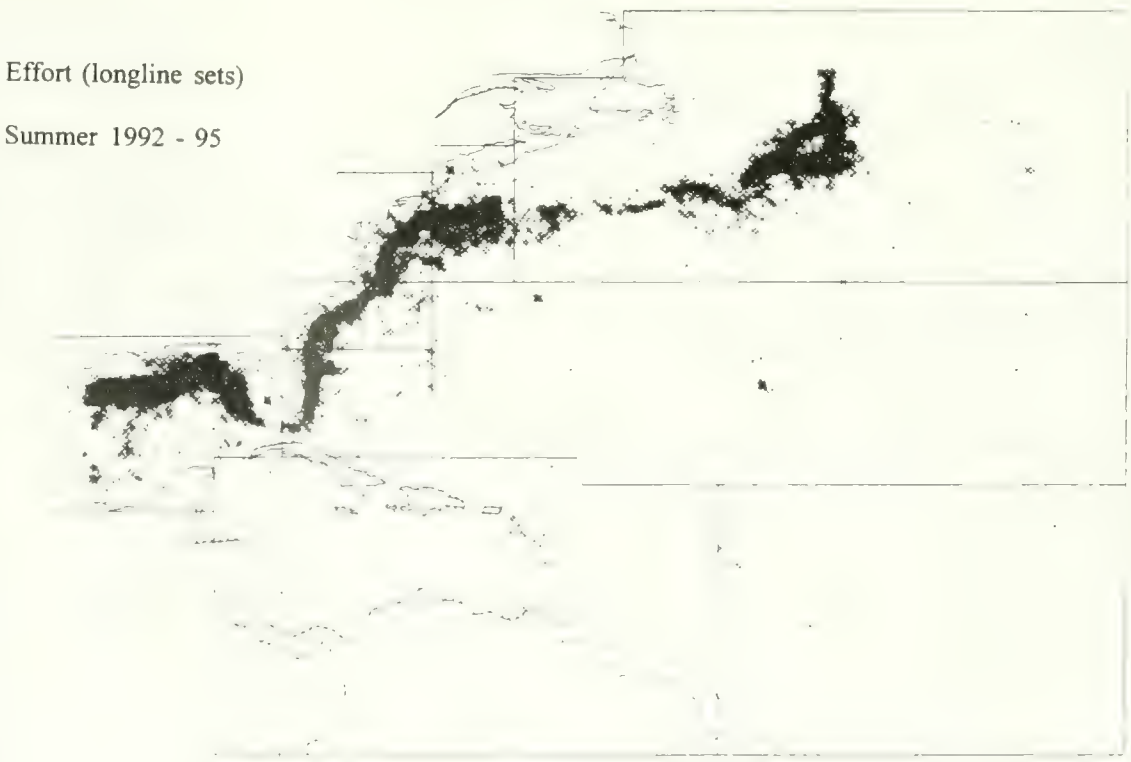


Figure 2

Pelagic longline fishing effort (sets), by season. Dashed line represents the 200-m isobath.

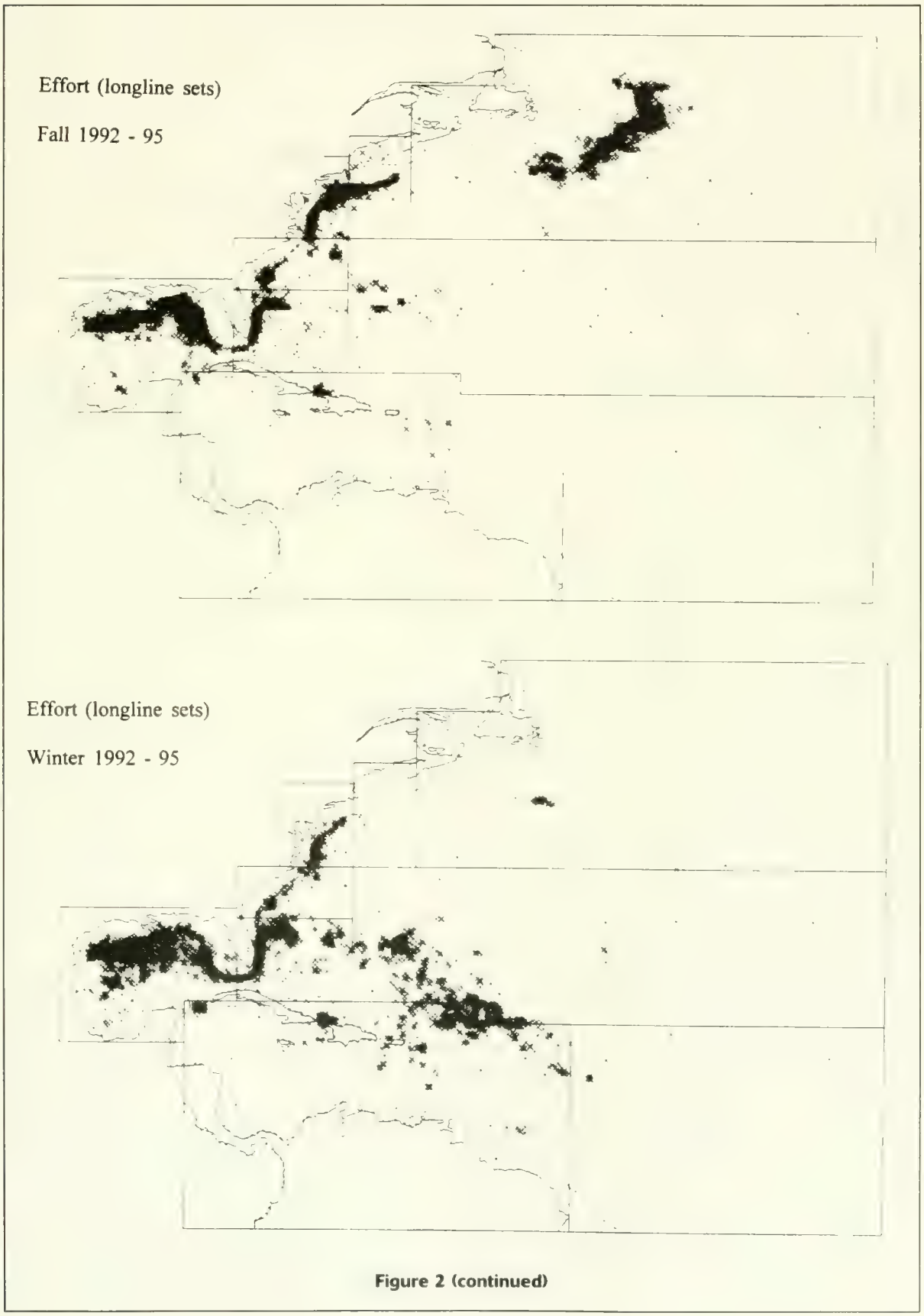


Figure 2 (continued)

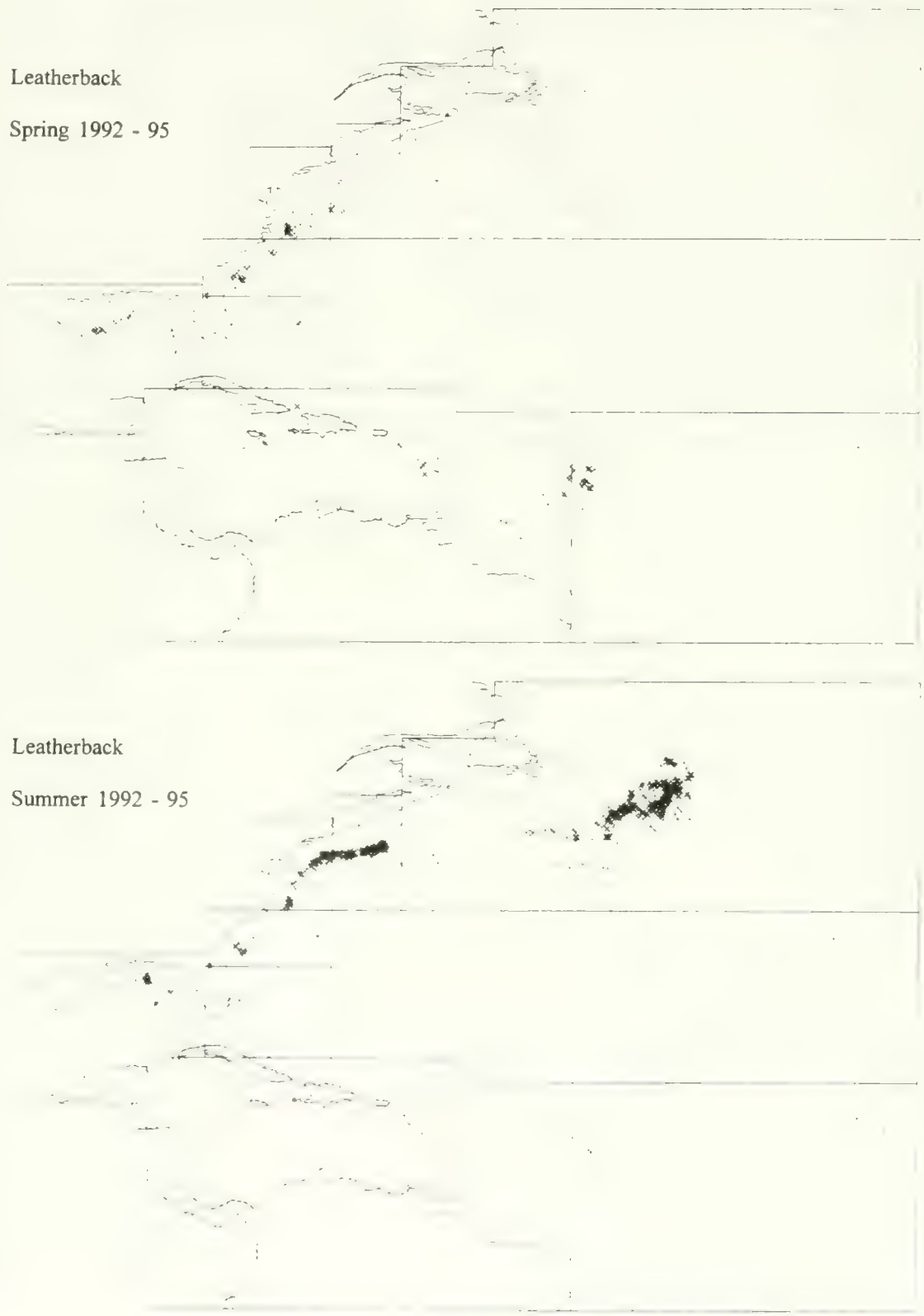


Figure 3

Leatherback sea turtle catches, by season (1992–95). Dashed line represents the 200-m isobath.

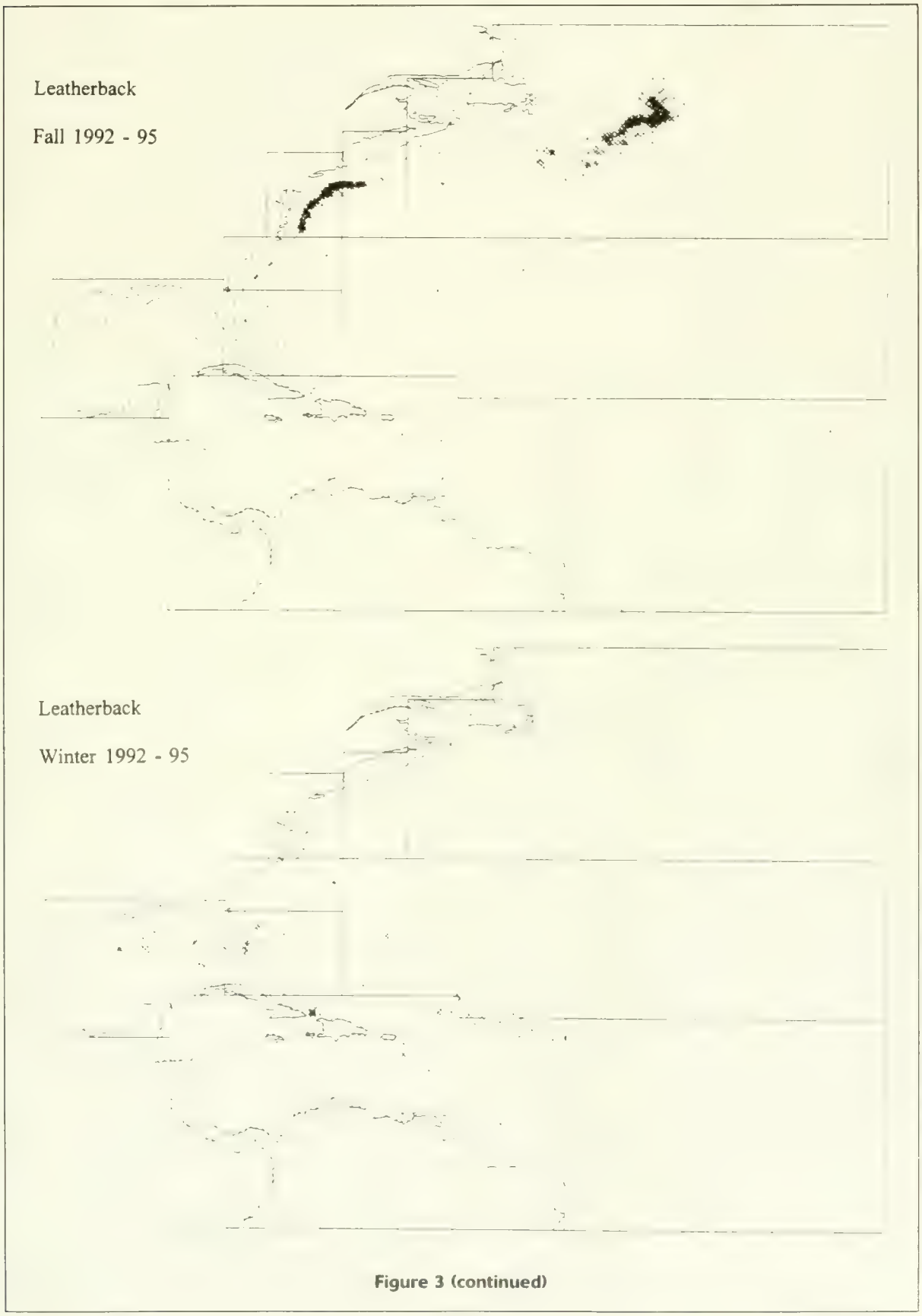


Figure 3 (continued)

Table 1

Leatherback (Lb) and loggerhead (Lh) turtle captures by the U.S. pelagic longline fleet, by NMFS fishing area, by month, for 1992–95.

	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8		Area 9		All areas combined	
Month	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh
01	16	12	4	6	4	2	0	0	1	4	0	0	0	0	0	0	5	4	30	28
02	17	7	12	1	2	3	0	0	0	7	0	0	0	0	0	0	2	3	33	21
03	13	24	8	4	6	2	3	1	6	7	0	0	0	0	4	2	0	1	40	41
04	4	4	7	3	2	1	3	2	1	3	2	1	0	0	1	1	0	0	20	15
05	5	1	1	4	1	1	7	4	13	3	5	3	0	0	11	1	0	0	53	17
06	1	1	3	9	2	1	6	3	22	24	35	49	40	39	3	0	1	0	113	126
07	2	0	10	5	0	0	3	3	19	10	48	62	170	233	0	0	0	0	252	313
08	3	0	10	7	1	0	2	2	32	24	48	14	152	212	0	0	0	0	248	259
09	0	1	0	1	1	1	4	2	76	11	30	4	167	310	0	0	0	0	278	330
10	1	1	2	5	1	0	0	3	84	8	12	6	56	123	0	0	0	0	156	146
11	3	1	3	2	0	1	2	0	7	5	0	4	8	19	0	0	2	0	25	32
12	4	4	3	1	3	1	0	0	1	2	0	0	0	0	0	0	5	1	16	9
Total	69	56	73	48	23	13	30	20	252	108	180	143	593	936	19	4	15	9	1264	1337

in the northeast distant (area 7). The overall CPUE for leatherback sea turtles caught by longline vessels using chemical light sticks was higher than the CPUE with vessels not using light sticks (Table 3), suggesting that the chemical light sticks might simulate bioluminescent gelatinous prey and attract leatherback sea turtles to the branchlines. Fortunately, these turtles tend to become entangled in the branchlines rather than consume baited hooks.

Leatherback sea turtles inhabit coastal and offshore pelagic waters in the North Atlantic Ocean (Pritchard, 1971). Morreale et al. (1994) speculated that they migrated along specific bathymetric contours outside the 200-m isobath, and Lutcavage (1996) proposed that they seek high concentrations of gelatinous prey along the oceanic fronts and meanders of the Gulf Stream. Shoop and Kenney (1992) reported that most were scattered along the continental shelf, except off Rhode Island in 1978, when a number of individuals were observed in association with a large concentration of *Cyanea*. Pelagic longline data, however, suggest that large numbers of leatherback sea turtles apparently also inhabit deep waters extending over the edge of the continental shelf outside the 200-m isobath from Cape Hatteras, North Carolina, to Georges Bank and the Grand Banks in the summer and fall months.

Loggerhead sea turtles

A total of 1337 loggerhead sea turtle captures were recorded in NMFS pelagic logbooks, 1992–95 (Table 1).

Table 2

Leatherback (Lb) and loggerhead (Lh) turtle captures by the U.S. pelagic longline fleet, by NMFS fishing area, by year.

	1992		1993		1994		1995	
Area	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh
1	19	12	17	6	8	11	25	27
2	20	9	25	8	12	6	16	25
3	3	2	6	4	11	3	3	4
4	10	2	3	6	7	5	10	7
5	147	30	68	13	29	32	18	33
6	81	26	54	51	19	19	26	47
7	84	59	67	33	105	278	337	566
8	0	0	0	1	3	0	16	3
9	5	0	5	5	4	2	1	2
Total	369	140	245	127	198	356	452	714

Total numbers of individual turtles caught are unknown because observer data indicate that some turtles may have been captured more than once. Year-round loggerhead sea turtle captures averaged 334 individuals per year (range: 127–714); June through November was the most productive period with 1174 (87.8%) captures. The mid-Atlantic Bight, northeast coast, and northeast distant waters (areas 5–7) were the most productive with a combined total of 1187 (88.7%) loggerhead sea turtle captures. Of these, the northeast distant area (7) accounted for 936 (70.0%) of the captures. Like leatherback sea turtles, logger-

Table 3

Leatherback (Lb) and loggerhead (Lh) turtle incidental CPUE from 1992–95 pelagic logbooks, by area, with (Y) and without (N) chemical light sticks. CPUE is turtle captures per 1000 hooks fished.

Area	Lights	Hooks	Lb Captures	Lh Captures	Lb CPUE	Lh CPUE
1	Y	1,036,600	66	54	0.0637	0.0521
1	N	101,716	3	2	0.0295	0.0197
2	Y	2,580,340	38	37	0.0147	0.0143
2	N	3,132,180	35	11	0.0112	0.0035
3	Y	1,389,240	23	13	0.0166	0.0094
3	N	45,773	0	0	0.0000	0.0000
4	Y	937,620	30	19	0.0320	0.0203
4	N	88,089	0	0	0.0000	0.0114
5	Y	1,523,970	154	53	0.1011	0.348
5	N	2,052,910	108	55	0.0526	0.0268
6	Y	1,356,540	132	83	0.0973	0.0612
6	N	835,484	48	60	0.0575	0.0718
7	Y	2,086,660	591	932	0.2832	0.4466
7	N	55,214	2	4	0.0362	0.0724
8	Y	51,593	18	4	0.3489	0.0774
8	N	1,285	1	0	0.7782	0.0000
9	Y	497,265	15	9	0.0302	0.0181
9	N	25,696	0	0	0.0000	0.0000
1–9	Y	11,459,800	1067	1204	0.0931	0.1051
1–9	N	6,338,350	197	133	0.0311	0.0210

head sea turtles were sporadically captured throughout the entire fishing area in the winter and spring and became abundant during the summer and fall in fishing areas 5–7 (Fig. 4). September was the most productive month with a combined total of 330 (24.7%) loggerhead sea turtle catches. Reported catches varied annually (Table 2). The mean curved carapace length (nuchal notch to tip of marginal) and weights of these captured sea turtles from the north east distant area (7) were 55.9 cm (SD=6.5 cm, n=98) and 22.1 kg (SD=11.1 kg, n=72). These turtles were smaller than coastal loggerheads from the northeastern United States (Lutcavage and Musick, 1985).

CPUE values indicated that loggerhead capture rates varied between areas (Table 3) and were highest for the northeast distant area (7). CPUE analysis indicated that the overall loggerhead sea turtle capture rates with light sticks were higher than the CPUE without light sticks (Table 3). Unlike leatherback sea turtles, loggerhead sea turtles readily consumed baited hooks. The fate of such hooked turtles is unknown, but they have been observed trailing multiple gangions; therefore some turtles previously hooked have remained actively feeding in the area.

Pelagic longline data indicate that loggerhead turtle distribution extends from coastal waters to the edge of the continental shelf from Cape Hatteras, North Carolina, to Georges Bank and the Grand Banks in the summer and fall months and also extends into deep waters off the shelf. These turtles are apparently able to move out of critically cold winter slope water to more hospitable southern waters. NMFS tagging data revealed that turtles hooked on their flippers were tagged in the spring in areas 6 and 7 and recovered in warmer winter waters in areas 4 and 2, respectively (NMFS[3]).

Conclusions

It is not surprising that pelagic longline fisheries incidentally catch turtles because fishing effort is concentrated either near the 200-m isobath or near interactions between major current systems. In these areas a variety of potential prey species (various nektonic organisms associated with *Sargassum*, as well as cephalopods, coelenterates, and schooling fish) concentrate and consequently attract tunas, swordfish, and sharks (Laurs et al., 1984; Maul et al., 1984; Kurowicki, 1987; Fiedler and Bernard, 1987; Podesta et al., 1993; Lutcavage, 1996). Aerial survey data off the eastern United States (Shoop and Kenney, 1992) and pelagic longline data presented here indicate that

[3] NMFS Cooperative Marine Turtle Tagging Program, Miami Laboratory, 75 Virginia Beach Drive, Miami, FL 33149.

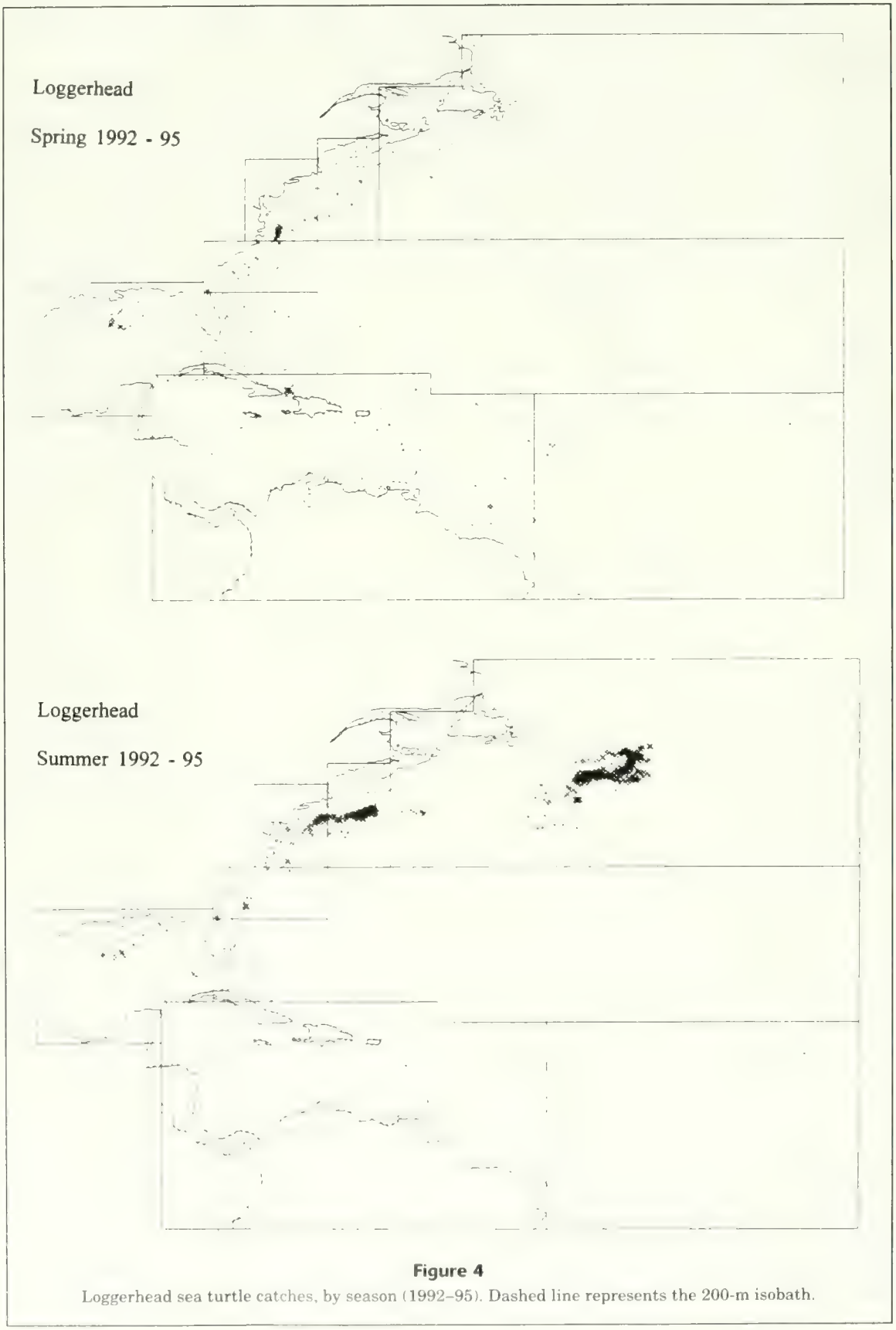


Figure 4

Loggerhead sea turtle catches, by season (1992–95). Dashed line represents the 200-m isobath.

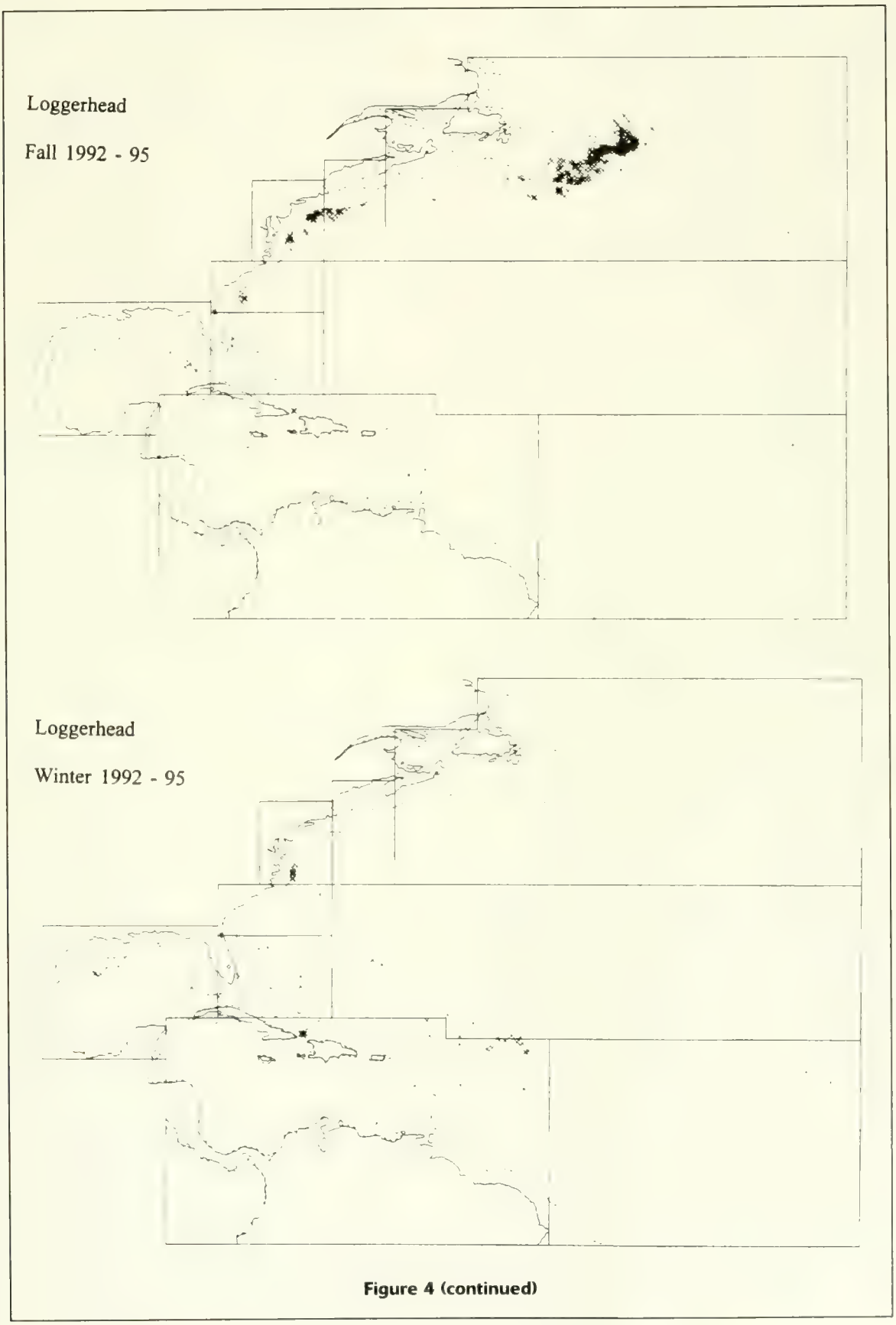


Figure 4 (continued)

leatherback and loggerhead sea turtles use the entire continental shelf, as well as the thermally dynamic waters off the continental edge.

The northeast distant fishing area (7) is particularly productive. The circulation and thermodynamics of fishing area 7 are very complex and provide a unique pelagic habitat. The Gulf Stream begins to meander northeastward off Cape Hatteras, and the western edge of the Gulf Stream eventually passes south of the Grand Banks as it turns eastward toward Europe. The thermodynamics of north Atlantic circulatory process near the Grand Banks is complicated (Schmitz and McCartney, 1993), and it is this interaction of cold slope water and warm Gulf Stream water that is productive for large pelagic fish and sea turtles. Moreover, the Gulf Stream spins off warm-core rings on the cooler northeastern slope water (Auer, 1987), where pelagic longline fishing is heaviest. These warm-core rings have been well studied, resulting in a plethora of published literature (Wiebe and McDougall, 1986). Unfortunately, these biological studies have concentrated on planktonic productivity and mesopelagic fishes rather than on larger pelagic apex predators; however, these rings affect the distribution and abundance of large pelagic fish, marine mammals, and sea turtles.

Fishery managers and sea turtle researchers need to develop conservation strategies that mitigate sea turtle and longline interactions. The high numbers of potentially lethal loggerhead sea turtle captures in the northeast distant area (7) during the summer and fall swordfish fishery particularly need to be addressed by fishery managers.

Acknowledgments

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Abstract.—Because of their tendency to return to natal streams, salmonid populations have often been viewed in ecological isolation, although the notion of an evolutionarily significant unit (ESU) recognizes dispersal on evolutionary time scales. We investigated the consequences of dispersal (straying) on an ecological time scale where straying creates a metapopulation structure for salmonid streams within an ESU. We developed a simple model for salmonid metapopulations, focusing on source and sink populations, and used the model to highlight the dangers of ignoring this structure in conservation efforts. We show that exactly the wrong conservation efforts may occur if metapopulation structure exists but is ignored.

The dangers of ignoring metapopulation structure for the conservation of salmonids

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The U.S. National Marine Fisheries Service (NMFS) Status Review of Coho Salmon (*Oncorhynchus kisutch*) from Washington, Oregon, and California (Weitkamp et al., 1995) formalized the agency's approach to defining both the boundaries and conservation status of distinct segments of salmonid populations for potential listing under the Endangered Species Act. With this approach, originally developed by Waples (1991), a population or group of populations is considered distinct if they are ". . . substantially reproductively isolated from conspecific populations," and if they are considered ". . . an important component of the evolutionary legacy of the species" (Weitkamp et al., 1995, p. 3). A distinct population or group populations is referred to as an evolutionarily significant unit (ESU) of the species.

For a group of populations to be classified as an ESU, the populations must be reproductively isolated from other populations but not from each other. An ESU also implies successful dispersal and reproduction between populations on an evolutionary time scale. A metapopulation is a group of populations (demes) linked by dispersal of individuals on a shorter ecological time scale such that dispersal affects both the genetics of the individual demes and their abundance and dynamics (Levins, 1969; Ruxton, 1996; Ruxton and Doebeli, 1996). To maintain consistency with the ecological literature, we have used the term "metapopulation" to refer to the group of populations or demes, and the term "population" or "deme" (often used interchangeably, see Policansky and Magnuson, 1998) to refer to one of the individual populations that make up the metapopulation. ESUs and metapopulations overlap on the continuum of population structures. Although a metapopulation will always compose part of, or the entire, ESU, an ESU does not have to contain any metapopulation structure. Dispersal between demes within a metapopulation must be great enough to affect the dynamics of the demes and the recolonization of habitats of extinct demes. Within an ESU, dispersal must only be great enough to contribute to the genetic make-up of component populations; it does not have to lead to recolonization events or affect the population dynamics.

Salmon typically return to their natal streams to spawn. However,

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some individuals stray to streams other than their natal one, and those streams may be inhabited or uninhabited by other conspecifc populations (Ricker, 1972; Quinn, 1993). Indeed, straying constitutes the process by which salmonids colonize new habitats (Milner and Bailey, 1989; Wood, 1995). Individuals that stray during the spawning migration may thus serve as the mechanism for dispersal between salmonid populations on both an evolutionary and ecological time scale.

Reliable estimates of the magnitude of straying are rare and span a wide range of values across and within species (Quinn, 1993; Pascual and Quinn, 1994). Quinn and Fresh (1984) documented a straying rate of 1.4% in their study of wild chinook salmon (*Oncorhynchus tshawytscha*) from the Cowlitz River Hatchery, Washington. Quinn et. al (1991) estimated hatchery straying rates ranging from 9.9 to 27.5% for five populations of autumn chinook on the Columbia River. Heard (1991) estimated that, in general, nearly 10% of wild pink salmon (*Oncorhynchus gorbuscha*) stray from their natal streams. Labelle (1992) estimated that approximately 4.7% of individual coho salmon strayed between nine separate streams along the coast of Vancouver Island, British Colombia, but that straying could be greater than 40% for some streams in some years. Genetic studies such as that of Gall et al. (1992) suggest that the average number of migrants exchanging genes per generation (Nm) in west coast Chinook salmon populations is on the order of 5–15 individuals.

Because the incidence of straying is common and the magnitude of straying is so variable, it is quite likely that metapopulation structure could exist for at least some salmonid populations. In fact, the National Research Council's report on Pacific Northwest salmonids recognizes that ". . . maintaining a metapopulation structure with good geographic distribution should be a top management priority to sustain salmon populations over the long term" (NRC, 1996, p. 8). Given the geographic scale of the straying documented in the previous studies, compared with the range of an ESU (note that the entire West Coast comprised only six ESUs), it is possible that a single ESU may even contain multiple metapopulations, as would be expected because ESUs are explicitly evolutionary constructs, whereas metapopulations are explicitly ecological constructs.

In this paper, we investigate the implications of metapopulation structure for conservation efforts given a variety of spatial scales. In particular, we identify the problems such structure could cause for managers if it left undetected. If one is concerned strictly with the risk of extinction for a species, metapopulation structure may be quite beneficial (Levins, 1970; Hanski and Gilpin, 1991; Hanski, 1994; Ruxton, 1996; Ruxton and Doebeli, 1996). Because the metapopulation occurs in patches (each of which contains a deme with its own probability of extinction) and because these demes are connected through dispersal, if any single deme becomes extinct, then there is a nonzero probability that the patch will be recolonized by individuals from another deme. Over time, an individual patch may therefore experience multiple extinctions and recolonization events. These events result in the metapopulation as a whole persisting far longer than any one of its individual demes. Potential problems arise when one is concerned not just with the risk of extinction but with the management (and therefore monitoring) of these populations.

In the most simple metapopulation model, one assumes that all demes, and the patches they inhabit, are identical (Levins, 1970). This, however, need not be the case, and in the real world, is likely not to be the case. One metapopulation model that takes such variation into account is the source-sink metapopulation model (Pulliam, 1988). In this model, sink habitats are patches where local mortality exceeds local reproduction (so that $R_0<1$ or $r<0$). In other words, without individuals immigrating to the patch, a sink population cannot sustain itself. Source patches, on the other hand, are patches where local reproduction exceeds the sum of local mortality and emigration (so that $R_0>1$ or $r>0$). Populations in source habitats can persist without the populations in the sink habitats, but the opposite is not true. There are no assumptions regarding the relative abundance of individuals between these source and sink patches. In fact, it is quite possible for the sink patches to have larger populations than source populations (Pulliam, 1988). For example, if competitively dominant individuals hold territories of fixed size (as is the case with some bird species), a source habitat would be highly productive, yet would have a constant population size because all subdominant individuals would be forced to disperse. If this dispersal rate into the sink habitats were greater than the natural rate of decline (the difference between births and deaths) in the sinks, then sink habitats could contain more individuals than the source habitats. In such a case, undetected metapopulation structure could lead managers astray.

When metapopulation structure (especially source-sink dynamics) exists, the abundance of a species in an area can be disconnected from the specific survivorship and fecundity rates of that area owing to the effects of immigration. If ignored, this disconnection poses two problems for managers, both of which are made worse if the jurisdiction of the manager does

not cover the complete metapopulation. First, if managers are looking strictly at the abundance of individuals, they could be lulled into a false sense of security. The size of the demes in the source and sink habitats could be relatively constant despite the fact that, without the demes in the source, the demes in the sink would become extinct. Brawn and Robinson (1996) uncovered this very scenario with Neotropical migrant birds in Illinois.

The second problem is even more insidious. If deme abundance is no longer a good indicator of habitat quality, managers could be led into conserving the wrong type of habitat (van Horne, 1983; Pulliam, 1988). Gowan and Fausch (1996) demonstrated how this could occur regarding the effects of habitat changes on the demography of a variety of trout species in Colorado, although they did not discuss their results in terms of metapopulations. Over an eight-year period (four generations of trout), Gowan and Fausch (1996) discovered that the addition of woody debris in treatment areas significantly increased the number of individuals and the total trout biomass in treatment areas in relation to the control areas. However, with the aid of fin marks (clipped fins) and individual tags, they discovered that survival, individual growth, and recruitment rates in the treatment areas were not significantly different from those in the control areas. Immigration from outside the study area to the treatment sites was solely responsible for the increase in abundance and total biomass. If Gowan and Fausch (1996) had not been able to account for immigration to the site, they would likely not have been able to discern the true effects of the addition of woody debris and would have likely mistaken increased density for increased habitat productivity (cf. Hunter, 1991). Although source-sink metapopulation structure was not the cause of these results, such an example demonstrates how reliance on abundance or density estimates can lead managers astray when immigration or emigration is not taken into consideration.

Those faced with the responsibility of managing salmonid populations may encounter these very problems and issues. In the remainder of this paper, we develop a model to help focus ideas about the potential dangers of undetected metapopulation structure for salmonid conservation.

Materials and methods

The model

The model is simple, and the form of the model was chosen for ease of comprehension. We found that even such a simple model was adequate to illustrate the possible consequences of ignoring metapopulation structure.

We considered a group of generic salmonid demes that reside in streams that are distributed evenly along some waterway but that are close enough so that straying between any of the two groups is possible (though not necessarily with equal probability). The scale was completely generic. The streams could be tributaries to a single river, rivers within a watershed, or even separate watersheds. Next, we numbered these streams consecutively along this waterway. Each deme was then indexed by the number associated with the stream in which it resides (e.g. deme 4 resides between deme 3 and deme 5 along this waterway). For computational purposes, we considered 10 streams, which is equivalent to a metapopulation consisting of 10 demes spread over 10 patches. Assuming that density-dependent effects could be ignored (which, except for Allee effects, would be the case for any recovering population), the fundamental variables are

$N(i,t)$ = the deme abundance in stream i in year t;
$r(i,t)$ = the per-capita reproduction in stream i in year t;
$s(j,i,t)$ = the number of fish that stray from their natal stream j to stream i in year t; and
f = the fraction of fish that stray from their natal stream (assumed equal for all demes).

For simplicity's sake, we assumed that strays have the same reproductive potential as nonstrays in a given stream. This assumption decreases the parameter space but does not affect overall dynamics of the model. It does, however, limit the direct applicability of our specific examples to streams that are relatively close in proximity, yet, as will be explained, does not diminish the danger for management at the watershed, basin, or even ESU level. By incorporating an additional parameter to account for the differential reproductive potential, some of the dynamics would simply have been dampened, making them more difficult to perceive. Therefore, the population dynamics for a deme are

$$N(i,t+1) = r(i,t)\left\{N(i,t)(1-f) + \sum_{j \neq i} s(j,i,t)\right\}. \quad (1)$$

As with differential reproduction, the assumption that there are more complicated population dynamics (e.g. Ricker stock-recruitment relationships) would not change the basic message of our paper but would make it harder to perceive. In a more compli-

cated model, or one designed for a nongeneric salmonid, the model would be indexed by generation time instead of year, but the potential problems described in this paper would still apply.

We assumed $s(j,i,t)$ is an exponential function of the distance between stream i and j (see Hanski, 1994). We assumed that the streams are evenly spaced along the waterway and numbered consecutively, so that the distance between stream i and stream j is proportional to $|i-j|$. Therefore, the number of individuals straying from stream j to stream i is

$$s(j,i,t) = \frac{N(j,t)fe^{-m|i-j|}}{\sum_{k \neq j} e^{-m|k-j|}} \quad (2)$$

where m defines the rate at which straying decreases with distance, and the denominator is a normalization so that all strays end up in a stream (i.e. none are lost to the system).

We assumed that per-capita reproduction rate of each deme is a function of some baseline rate of per-capita reproduction that is equal for all streams (e.g. ocean conditions and harvest) plus a function of a component of the habitat that contributes positively towards per-capita reproduction (e.g. width of the riparian zone) and a function of a component of the habitat that contributes negatively to per-capita reproduction (e.g. road density). If z_0 is the baseline per-capita rate of reproduction and $z_1(i,t)$ and $z_2(i,t)$ are the amounts of the beneficial and detrimental habitat components for stream i in year t, then the per-capita rate of reproduction for stream i in year t is modeled as

$$r(i,t) = z_0 + g\left\{1 - e^{-z_1(i,t)}\right\} - b\left\{1 - e^{-z_2(i,t)}\right\} \quad (3)$$

where g = the maximum increase in the per-capita reproduction due to the beneficial habitat component; and

b = the maximum decrease in the per-capita reproduction due to the detrimental habitat component.

As $z_1(i,t)$ increases, $e^{-z_1(i,t)} \rightarrow 0$, so that the effect of the beneficial habitat component approaches an asymptote at g. Similarly, the detrimental habitat component approaches an asymptote at b. Therefore, $r(i,t)$ is constrained to lie between z_0-b and z_0+g. When $r(i,t)(1-f) \geq 1$, the deme is a source population (rate of change due to per-capita reproduction counteracts the rate of change due to emigration); when $r(i,t)(1-f) < 1$, the deme is a sink population (it can not sustain itself without immigration from other streams).

To include the effects of temporally varying environments, we added

$$q\sin\left(\frac{2\pi t}{w}\right)$$

to the per-capita reproduction. This causes per-capita reproduction to change sinusoidally with a maximum change of $2q$ with a w-year period. Such oscillations could be due to events such as El Niño (Pearcy, 1992) and essentially represent changes in the baseline conditions (z_0) over time.

Simulations

We set the baseline per-capita rate of reproduction with $z_0=1$, $g=0.2$, and $b=0.15$. Thus per-capita reproduction was constrained to $0.85 \leq r(i,t) \leq 1.2$. We drew the $z_1(i,0)$ and $z_2(i,0)$ from a gamma distribution with parameters 1 and 1 (Hilborn and Mangel, 1997).

We set $f = 0.05$ for all populations. This value lies within the ranges found by most of the previously mentioned research on salmonid straying rates. Streams were labeled as sources and sinks on the basis of their initial per-capita rate of reproduction given this straying rate. Therefore, a source population was one with an initial per-capita rate of reproduction greater than or equal to 1.05, and a sink population was one whose rate was less than 1.05. With these parameters, about 40% of the streams were sources and 60% were sinks, as would be the case for a heavily impacted region (Fig. 1). We set $m = 0.1$.

The initial deme abundance for each stream was assumed to be proportional to the initial per-capita reproduction rate for that stream, even though such relationships may not hold over time (van Horne, 1983). As such, the initial deme abundance, $N(i,0)$, was set equal to $100r(i,0)$. We simulated each metapopulation over a 100-year period, using four scenarios with at least 150 replications for each scenario:

1 All parameters were constant over the 100-year period;
2 Starting in year 5, for all initial source populations ($r(i,0) \geq 1.05$), the good habitat component (z_1) decreased by 5% of its value from the year before, and the bad habitat component (z_2) increased by 5% of its value from the year before.
3 Same as scenario 2, except that all habitats with $r(i,0)>1$ were degraded.
4 Temporally varying environment was incorporated into scenario 2. In this case, the baseline per-capita rate of reproduction (z_0) oscillated between 0.95 and 1.05 over a 20-year period.

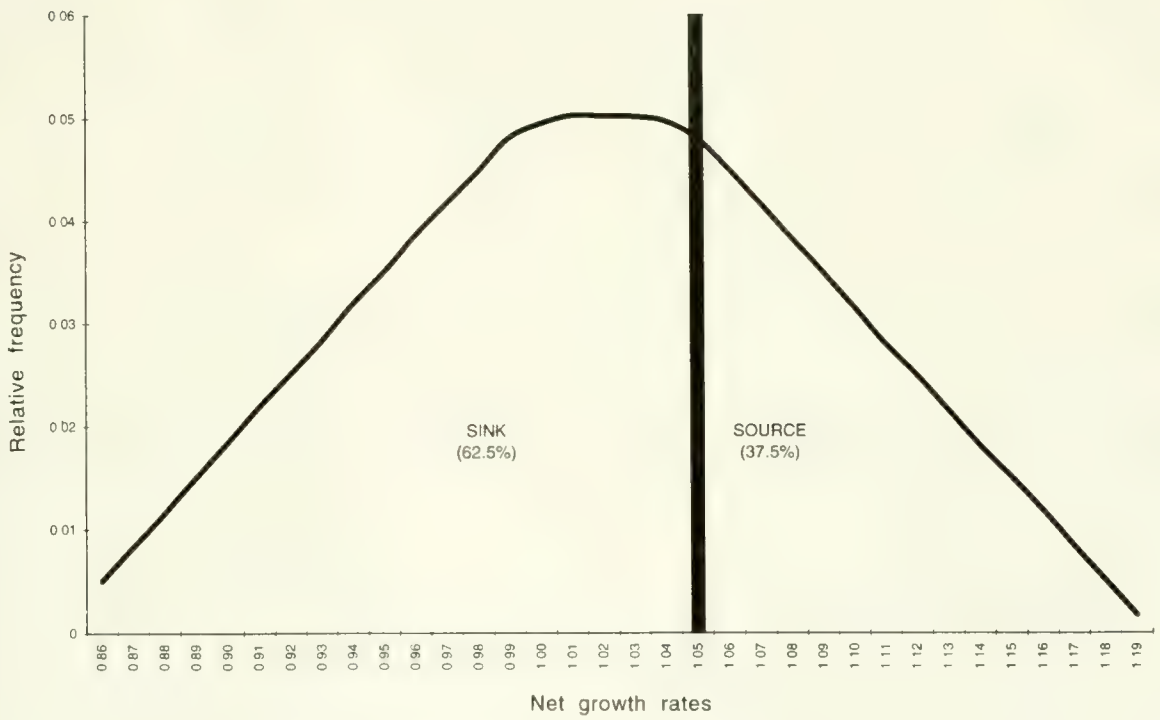

Figure 1

Distribution of net growth rates. Our model generates variation in per-capita growth rates in local populations. A population is a source if its per-capita growth rate exceeds 1.05 and is a sink otherwise.

Results

When habitats are constant over the simulation period, exponential growth occurs 98% of the time. Because no density dependence was incorporated in the model, demes in the source habitats increased exponentially, as did the number of strays from these sources. Such a situation could occur if, for instance, harvesting pressure was decreased on a deme that had been severely overharvested in the past (leading to low abundance) but whose habitat was relatively pristine (maintaining high productivity). This results in all dynamics in the sink populations being obscured by the massive number of immigrants.

It is possible that all the streams constitute sinks (all $r(i,0) < 1.05$); this occurred in 1.3% of the simulations. In this case, there is still the possibility that the metapopulation as a whole could persist for decades before all populations began to decrease (Fig. 2). The reason for this persistence is that individuals that stray are lost only to their natal stream, not to the metapopulation as a whole. The case shown in Figure 2 results when the losses due to some habitats (where $r(i,t)<1$) are nearly offset by production in other habitats (where $r(i,t)>1$). Forty percent of the all-sink metapopulations produced populations that did not decrease over the course of the 100-year simulation. If we had incorporated a parameter to represent decreased reproductive success of strays, the incidence of nondecreasing, all-sink metapopulations would have been lower.

In scenario 2 (Fig. 3), the source populations (demes 3, 4, and 5) initially increased exponentially but eventually began to decrease as the habitat degradation increased. Habitat degradation leads to peaks in local deme abundance (Fig. 4A). The mode of this distribution was around year 20 despite the fact that habitat degradation began in year 5. Furthermore, in over 3% of the sources, deme sizes increased throughout the 100-year simulation.

The population trajectories for the sink habitats were less intuitive (Fig. 3). None of their habitat components changed, yet some demes increased (deme 1) or stayed constant (deme 9) over a number of decades, whereas others decreased. The result depends on the proximity to sources (noting that deme number translates to the location of the deme along the waterway), the per-capita rate of reproduction in those sources, and the sink's own per-capita rate of reproduction. Over 9% of the sink habitats never attained

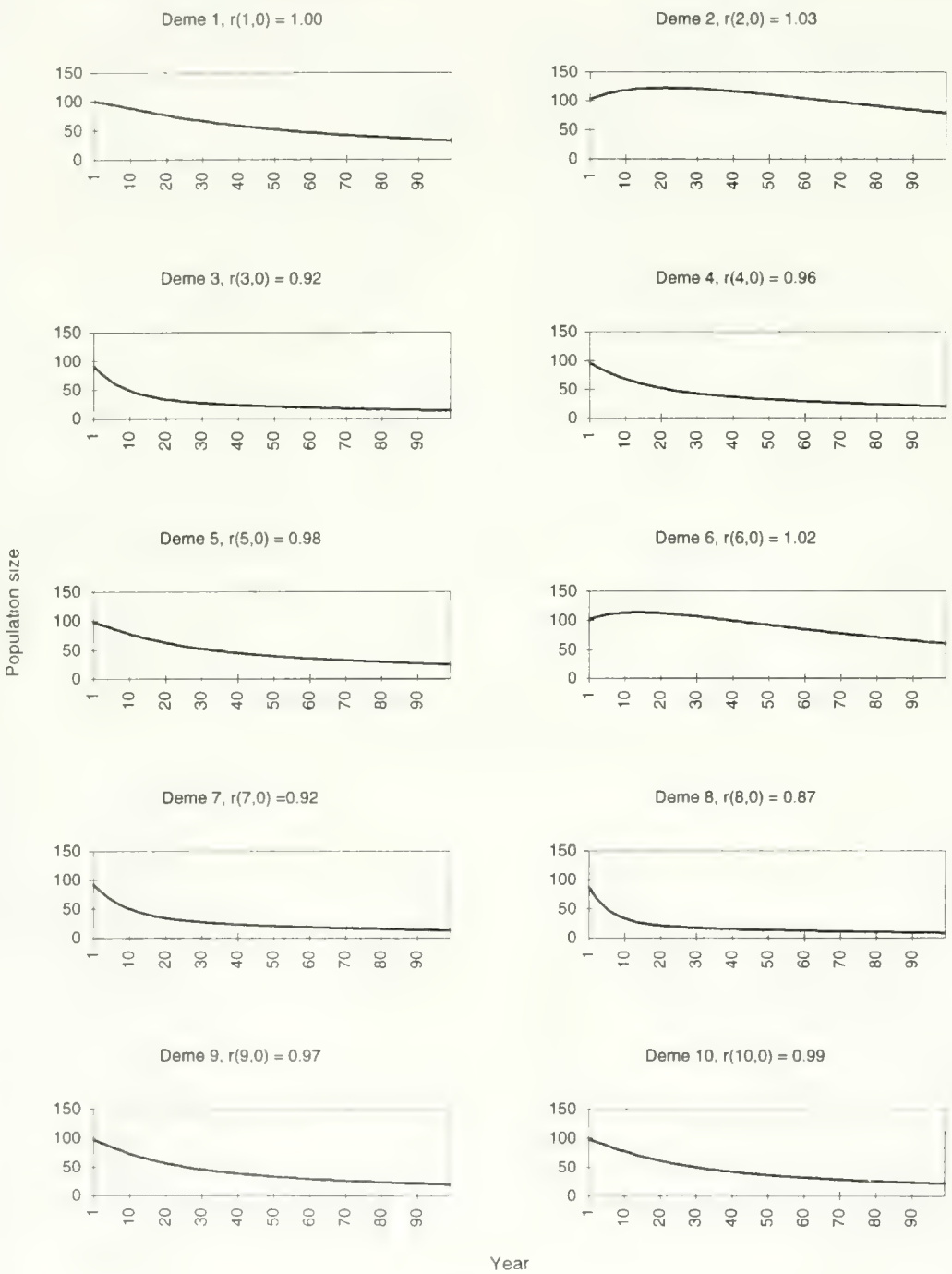

Figure 2

The dynamics of the metapopulation when all local populations are sinks. With scenario 1 or 2 (see "Simulations" section), metapopulation structure and dispersal actually lead to an increase in some population sizes over the short term, before they decline

deme sizes larger than their initial deme size, but nearly 7% of the demes in sink habitats continued to increase over the entire simulation (Fig. 4B). The fact that deme sizes in some sink habitats do not decrease over the simulation period is a result of the time of the simulation in relation to the rate of habitat degradation in the sources. If the simulations had been longer, all habitats would eventually have reached

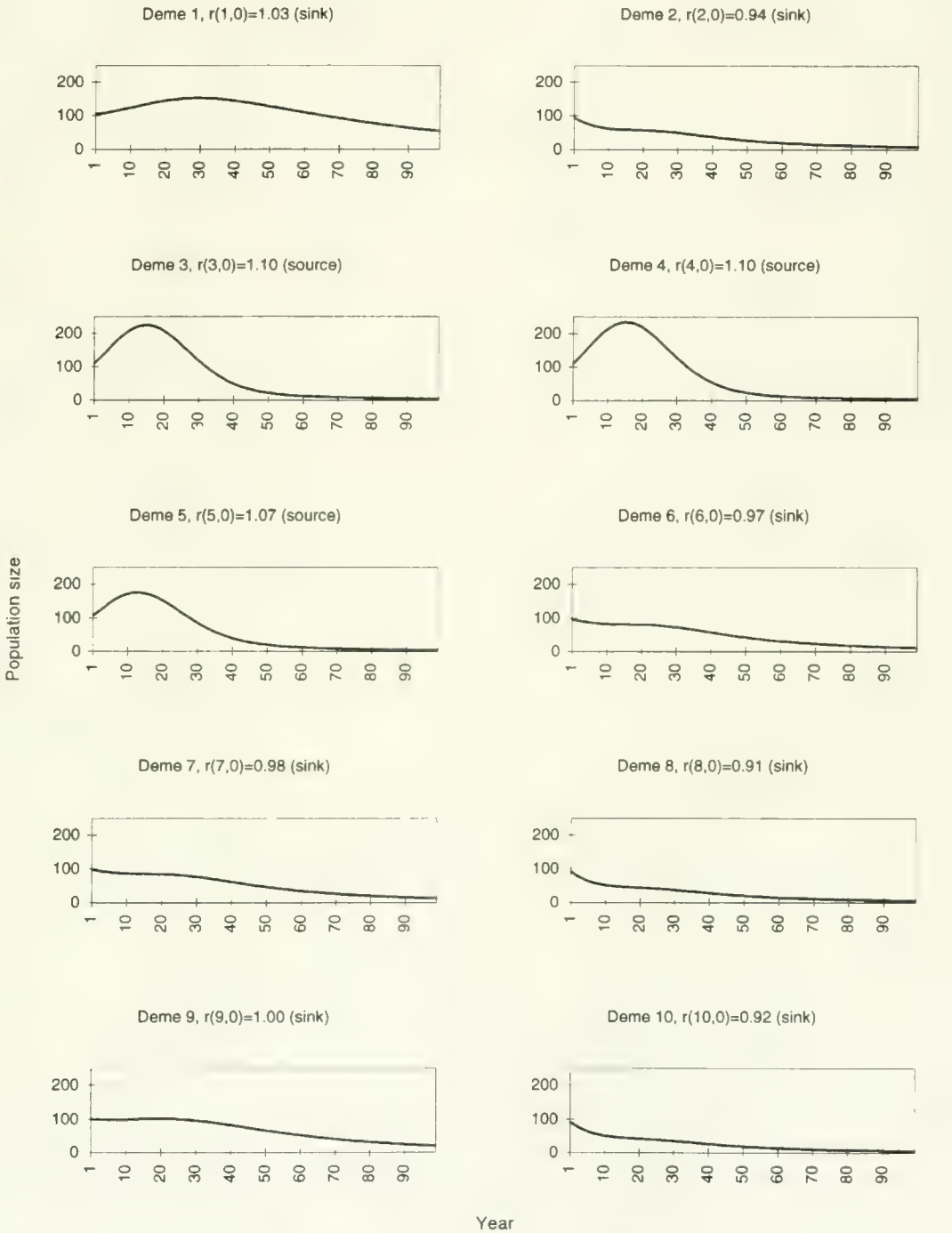

Figure 3

The dynamics of the local populations when some are sources and some are sinks. With scenario 2 (see "Simulations" section), as habitat degradation proceeds (starting in year 5), habitats for source populations slowly become degraded and end up as sinks.

the state of being sink habitats, which would then have resulted in only a few instances of sustained or increasing metapopulations (as described above). Because the number of migrants from one deme to another decreases with distance, the year in which the maximum deme size is attained by the sink decreases as the distance from a source increases; thus the sinks rely on source populations for their viabil-

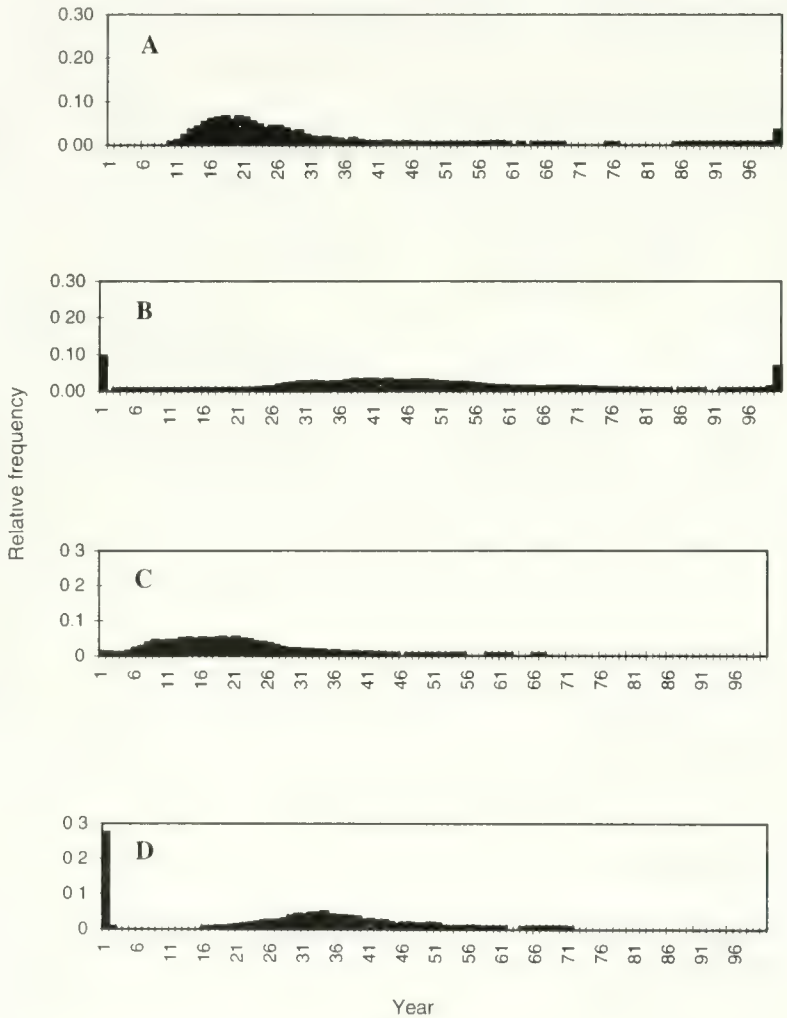

Figure 4

Proportion of sources (**A** and **C**) and sinks (**B** and **D**) attaining their maximum population size in a given year for scenario 2 (A and B) and scenario 3 (C and D). (A) Habitat degradation causes source population size to peak sometime after year 5, although a few populations maintain themselves throughout the 100-year simulation period. (B) About 10% of the sink populations attain maximum size at the start of the simulation. A few attain maximum size at the end of the simulations, but most attain maximum size around year 40. They are supported by source populations. (C) The frequency distribution of peaks in population size for populations with initial per-capita growth rate >1. Compare with Figure 4A. (D) Most populations with initial per-capita growth rate <1 attain peak size at the start of the simulated period. Compare with Figure 4B.

ity (Fig. 5). The variance about these points is due not only to the per-capita reproductive rate of the sink and its nearest source but also to a failure to account for the location of any other sources that may be of equal or greater distance from the nearest source and thus contribute to the sink's dynamics.

When all demes with initial per-capita growth rates greater than one are affected by habitat degradation, declines in deme size occur more frequently, more rapidly, and sooner than in the previous case (Figs. 4 and 6) In this scenario, 100% of the demes were driven towards extinction.

When an oscillating environment is incorporated, the general trends in abundance are similar to those in scenario 2, but now each deme also tracks the environment (Fig. 7). All sources (demes 3, 5, and 7)

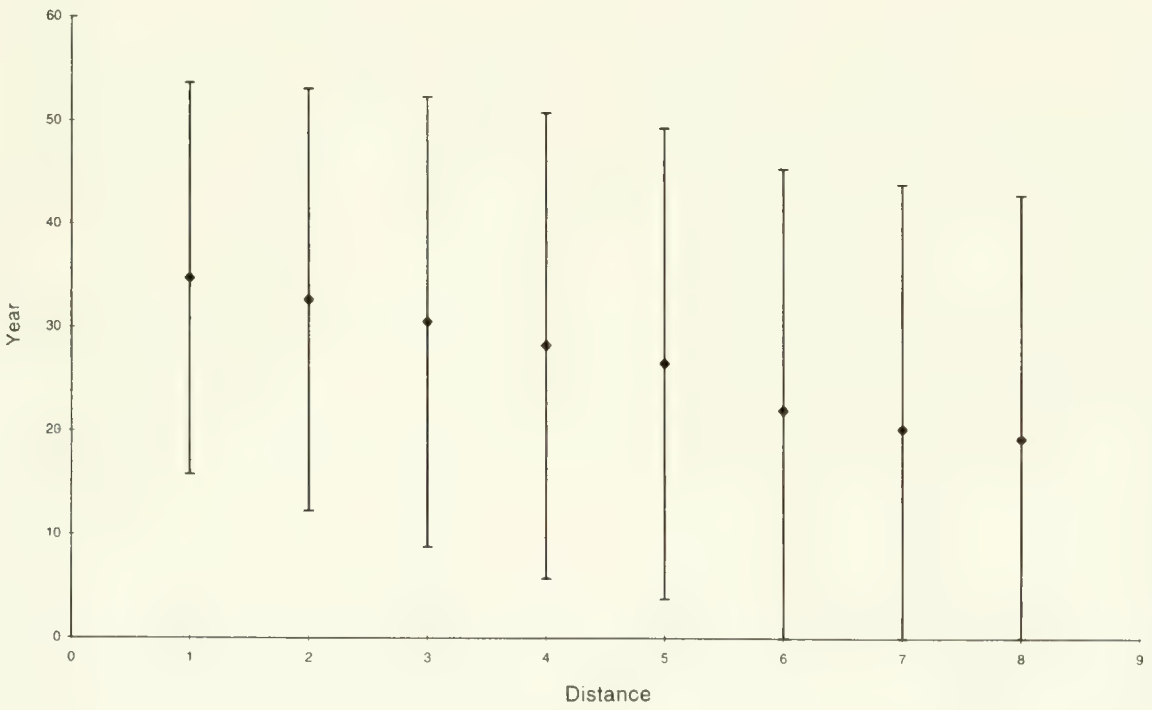

Figure 5

Average year in which sinks attained their maximum population size as a function of the distance to the nearest source. The year in which a sink population attains its maximum size depends upon the distance to the closest source, but there is considerable variation in dependence. Error bars represent one standard deviation.

initially increase but then decrease as habitat degradation progresses. Some demes in sink habitats, such as demes 1 and 4, were relatively stable if not increasing over a fair portion of the simulation period before declining towards extinction.

Discussion

Undetected metapopulation structure in salmonid populations may obscure the signals that managers use to determine the need for convervation action. Abundance trends, either absolute numbers or simple indices of abundance, constitute the primary input into analyses used for fisheries management and decision-making (Hilborn and Walters, 1992). The majority of these techniques assume that the population in question is a closed system, that any immigration or emigration can be considered negligible.

In California, Oregon, and Washington, estimates of population or run size for most salmonid species are commonly based on number of spawning fish or redd counts taken from index reaches or streams (WDFW, 1994; ODFW, 1995; Weitkamp et al., 1995). The absolute numbers of spawning fish or redds counted in these index streams, which incorporate only a minute portion of the available spawning habitat within the watershed, are then used to extrapolate watershed- or basin-level abundance estimates, the very estimates upon which managers base their decisions. In fact, in their discussion on the data available for assessing the population size and risk of extinction for coho salmon along the west coast of the United States, Weitkamp et al. (1995, p. 106) stated ". . . where [stream] surveys were conducted, they are the best local indication we have of population abundance trends." Index reaches and streams such as these are precisely the situation modeled in the specific examples discussed in this paper; straying between these reaches is likely and differential reproductive success between strays and natal fish may not occur. The NMFS's analysis of coho salmon populations considered short- and long-term trends in abundance to be the main indicators for the risk of extinction but avoided using estimates based on index streams (Weitkamp et al., 1995). Using the trends in abundance for an entire ESU, Weitkamp et al. (1995) attempted to avoid the problems associated with the

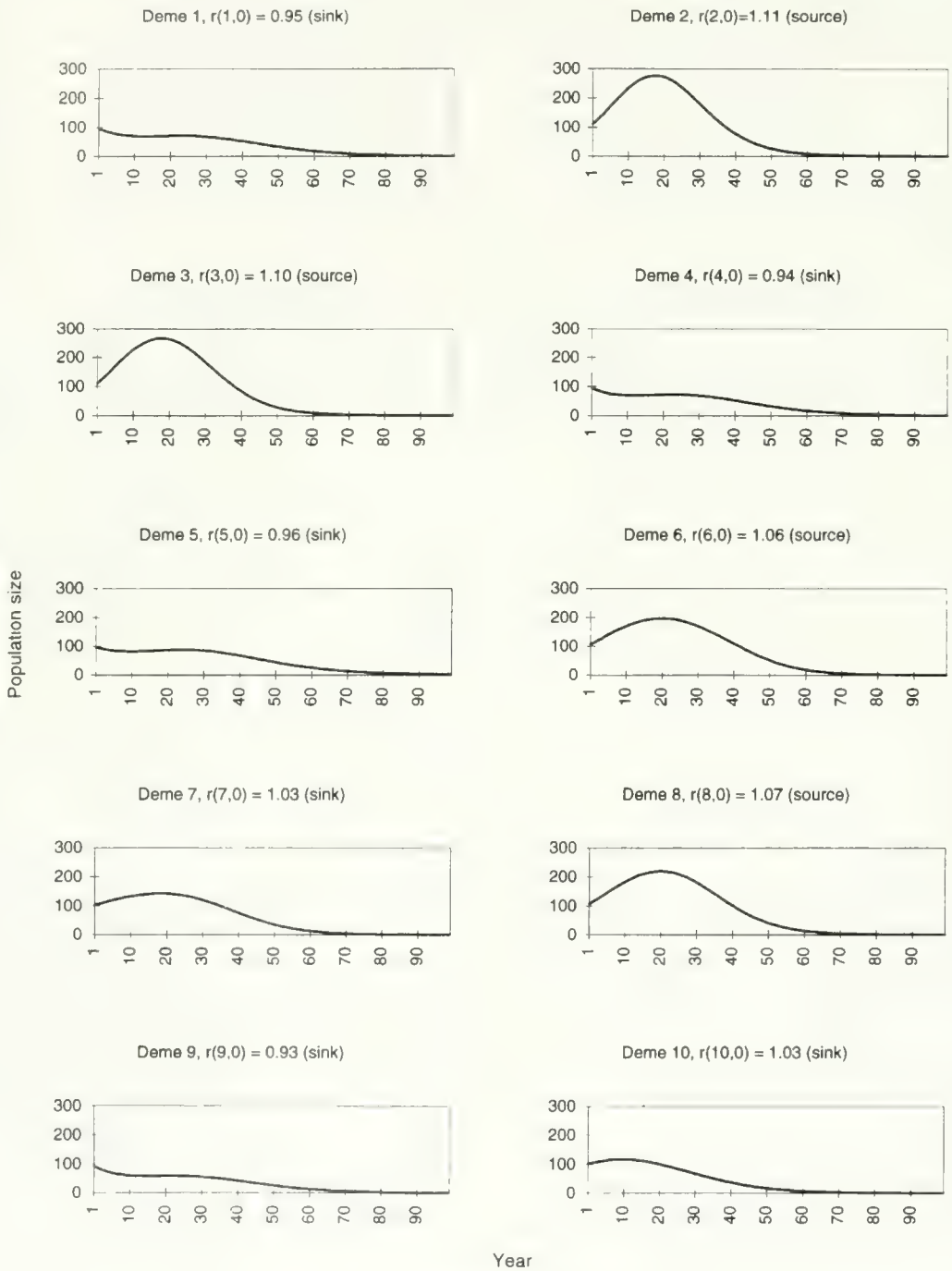

Figure 6

The local population dynamics when all populations with initial per-capita growth rate >1 are subject to habitat degradation (scenario 3 in "Simulations" section). Compare with Figure 3.

assumption of a closed-system. However, depending on the time scale of the data available and the decrease in reproductive success for strays, undetected metapopulation structure could still cause problems. The second problem arises because metapopulation structure can disconnect the abundance-habitat quality relationship. This could lead managers to make erroneous inferences regarding the habitat requirements for a species. The

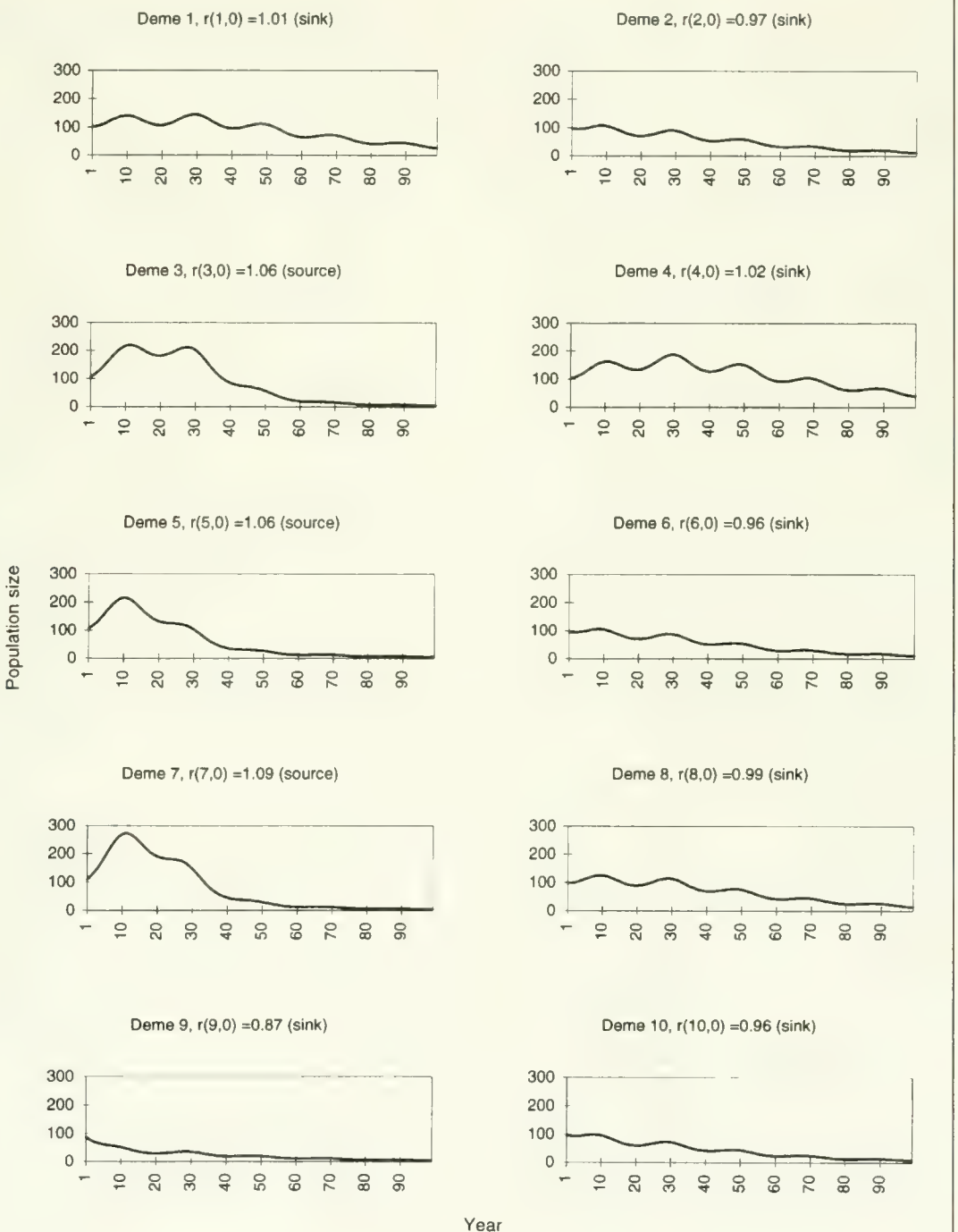

Figure 7

When z_0 varies (scenario 4 in "Simulations" section), the local population sizes reflect such variation. Compare with Figure 3.

sample metapopulations from the simulations provide demonstrations of how this may occur.

Figure 3 demonstrates one example where metapopulation structure could obscure management signals. Keep in mind, there is neither density dependence, observation error, nor stochasticity in the population dynamics, and a deme could represent an index reach (conforming to our uniform reproductive

success assumption) or an entire stream (where the uniform success assumption may be less accurate). If a manager had the entire time series data for all of the demes, the problem (though not the solution) would be evident; all demes would have declined significantly. Suppose, however, the manager is currently in year 30, and has only 25 years of data (years 5–30). Over that time period, all demes in sink habitats would be relatively stable or decline only slowly, even though none could sustain themselves without immigrants. In fact, deme 1 had been increasing until year 30. The demes in the source habitats, however, showed the effects of habitat degradation. Seeing these trends, the manager could perhaps stabilize these demes and thus inadvertently save the entire metapopulation. Still, the true risk for the sink populations would be unknown to the manager. The sink populations would appear stable not because they were in good condition but rather because of their interconnectedness with one another and the source populations.

Rieman and McIntyre (1995) suggested that a similar process is occurring with bull trout (*Salvelinus confluentus*) populations in Idaho. Although bull trout were found to use small streams, they do so only at a very low frequency. Rieman and McIntyre (1995) concluded that the presence of trout in these streams may be influenced by habitat preference but that these populations depend on dispersal of individuals from larger streams for their sustainability.

The addition of a varying environment clouds the picture even more (Fig. 7). The manager must now distinguish between decreases due to environmental factors and decreases due to factors that can be controlled. Imagine a manager starting in year 1. How can one recognize that the metapopulation is collapsing due to anthropogenic effects and not simply to environmentally induced effects? When would the alarms sound? Probably not until sometime after year 30, when even the most historically productive demes do not begin to increase. Seven out of ten of the demes could not maintain themselves without immigration, there is neither observation error nor stochasticity, and it would still take over 25 years of habitat degradation before the problem was noticed and the alarms sounded.

These problems become even more serious when management boundaries do not coincide with metapopulation boundaries or when only a portion of the metapopulation is used as index streams, as is likely the case. In such a situation, a manager will be concerned with, have jurisdiction over, and maybe have data on some subset of the metapopulation. Returning to Figure 3 (where managers do not have to deal with fluctuating environments), imagine if a manager had responsibility, and therefore data, for only demes 6, 7, 8, 9, and 10, which are nevertheless a significant portion of the metapopulation. Between years 5 and 30, all demes were relatively stable, despite the fact that without immigration, even the most productive deme (deme 9) would decrease at a rate of 5% per year. After year 30, all these demes begin to decline. The manager would, of course, begin looking at these demes to try and see what was causing this decline; a good manager would try to find what had changed. In fact, nothing has changed with these demes; they have exactly the same rates of per-capita reproduction and straying over the entire simulation. Only the number of immigrants has changed. Without looking beyond their own jurisdiction or at streams other than the index streams, managers would not find the true cause for the change in dynamics. As the number of demes that are used as index streams or that lie within a manager's jurisdiction decreases, the likelihood of such a problem increases. Considering that over 90% of the sink populations increased in size during some portion of the simulation time horizon (i.e. their maximum size was reached sometime after year 1, Fig. 4B), the fate of sink populations has as much, if not more, to do with the health of the demes in other habitats as with the quality of their own habitat.

Another problem associated with undetected metapopulation structure arises directly from this last example. A manager may see a change in the dynamics in the populations and look for the cause. However, the cause of this change is outside the manager's jurisdiction or data set; it is not local. If the manager looks only for local causes for this change, she or he is likely to find some variable that is correlated with this cause and possibly infer local causality. Having attributed causality to a local variable, the manager would likely start funding projects to fix the perceived problem in the correlated variable. If one is lucky, very lucky, this variable might have some relationship to the per-capita reproductive rate and thus improve the situation a bit. This might, then, slow the rate of decline, but because it is not the true cause of the decline, the situation would likely continue to deteriorate. How much of a manager's limited resources might be spent on such activities before the true causal relationship was discovered? The study by Gowan and Fausch (1996) suggests that this problem may be occurring with habitat enhancement projects for trout in Colorado; managers promote the addition of woody debris in streams because it increases trout density, even though it does not seem to improve the demographic parameters of the population.

Including density dependence (as in Ricker stock-recruitment relationships) and observation or pro-

cess uncertainty (Hilborn and Mangel, 1997) in the model will not change any of the main conclusions. These factors will make recognizing the problem even more difficult, as is the case in the real world. To uncover metapopulation dynamics, one must explore two aspects of each population's life history in reference to its habitat: dispersal (in the form of immigration and emigration) and the per-capita reproductive rate (defined by survival and reproduction). Watershed-scale estimates of these rates, however, are not appropriate. Given their reliance on index stream counts, managers must know the rates of immigration, emigration, and reproduction specific to that stream to be able to understand the true dynamics of that stream. The dispersal of individuals is important to determine the extent of the metapopulation structure. The focus should be both on absolute numbers as well as on the effective migration rates that account for differences in survival and productivity between the residents and the migrants. Survival and reproduction estimates (the components of the per-capita reproductive rate) will allow the manager to assess the potential importance of the metapopulation structure (i.e. to define sources and sinks). As long as the risk exists for abundance and density estimates to be disconnected from habitat quality and per-capita reproduction, all the above information is required to make an accurate assessment of the conservation status of the individual demes and to choose the appropriate management actions.

A great deal of time, money, and effort is currently directed toward the conservation and improvement of salmonid populations and their habitats. The NMFS report alludes to the fact that metapopulation structure may exist between some salmonid populations, and the NRC (1996) report lists the maintenance of metapopulation structure as one of its most important recommendations. Without investigating the possibility of metapopulation structure, researchers, managers, and policy makers are setting themselves up to fall into the traps described above: that of either not seeing a problem that may exist or, if they do see it, not knowing the true causes of such a problem.

Acknowledgments

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Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*

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Abstract.—*Polyprion oxygeneios* (family Polyprionidae) is fished commercially and recreationally in the southern Indian and Pacific Oceans. Estimates of growth rate, age at maturity and recruitment, and longevity are required for fishery management. We used thin otolith sections to age *P. oxygeneios* from New Zealand, where it is known as hapuku. Growth bands were difficult to count, leading to low counting precision and, for some age groups, to a small between- and within-reader ageing bias. These problems, however, had little effect on the shape of growth curves fitted to length-at-age data. An oxytetracycline injection experiment supported our hypothesis of annual deposition of an opaque-hyaline band pair, but further validation is required. Independently derived von Bertalanffy growth curves (from length-frequency data) and growth-rate estimates (from tag-recapture data) for young hapuku agreed well with estimates from length-at-age data.

Juvenile hapuku are pelagic and most switch to a demersal habitat at around 50 cm total length and at an estimated age of 3–4 years. They probably recruit to commercial trawl catches at about the same age. Female hapuku appear to grow slightly faster than males. Both sexes mature at about 10–13 years. The longevity of hapuku is uncertain, but some individuals probably live longer than 60 years.

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Fish. Bull. 97:227–242 (1999).

Polyprion oxygeneios (Schneider, 1801) (family Polyprionidae) is a large demersal fish that inhabits temperate and subtropical waters of the southern Indian and Pacific Oceans (Roberts, 1986; Fig. 1). It supports significant fisheries off the Juan Fernández Islands, Chile, and off New Zealand and is an important bycatch in south-east Australian longline fisheries (Johnston, 1983; Pavez and Oyarzún, 1985; Pizzaro and Yáñez, 1985; Kailola et al., 1993; Annala and Sullivan, 1997). The closely related wreckfish, *P. americanus* (Bloch and Schneider, 1801) is found in the North and South Atlantic Oceans, Mediterranean Sea, southern Indian Ocean, and south-west Pacific Ocean (Roberts, 1986; Sedberry et al., 1994) and supports fisheries throughout its range (Sedberry et al., 1994, 1996).

The ability to age *Polyprion* species is essential for proper management of their widespread fisheries, because it will enable determination of growth rates, ages at maturity and recruitment, longevity, and natural mortality rates. Previous attempts to age the two species have had limited success. Age and growth of *P. oxygeneios* have been estimated from otolith band counts in New Zealand (McDougall, 1975) and from scale annuli counts in Juan Fernández Island (Pavez and Oyarzún, 1985). A study on the age and growth of *P. americanus* from the north-west Atlantic is currently underway (Sedberry et al., 1994, 1996; Manooch and Potts[1]). However, otolith bands have proven difficult to count in both species, scale annuli are unreliable for older fish, and the ageing techniques have not been validated.

In New Zealand, *P. oxygeneios* and *P. americanus* are managed as a single species-unit in the Quota Management System (QMS) (Paul and Davies, 1988; Annala and Sullivan, 1997). Both species are fished commercially and recreationally throughout New Zealand. They are highly sought after, but catches are relatively low. Commercial landings of both species combined peaked at 2700 t in 1983–84, but since the introduction of the QMS, they have been constrained by quotas to less than 1500 t per year (Annala and Sullivan, 1997). Despite these quotas, commercial line and set-net fisheries for *Polyprion* species have been seasonally important for small inshore fishing vessels in many parts of New Zealand. Annual recreational landings were about 500 t in 1991–94 (Annala and Sullivan, 1997).

This paper addresses age and growth in New Zealand *P. oxy-*

[1] Manooch, C. S., and J. Potts. 1997. National Marine Fisheries Service, 101 Pivers Island Rd, Beaufort, NC 28516. Personal commun.

Figure 1
Hapuku, *Polyprion oxygeneios* (63 cm TL).

geneios, hereafter called hapuku. However, our results are also relevant to other populations of *P. oxygeneios* and, because both species of *Polyprion* have similar otolith structure, our results should also assist in the interpretation of otoliths of *P. americanus*. We used thin otolith sections to age hapuku and attempted to validate ages using oxytetracycline (as a time marker) and otolith marginal state analysis. We also obtained independent growth rate estimates from length-frequency and tag-recapture data for comparison with growth rate estimates derived from length-at-age data.

Materials and methods

Otolith ageing

Sagittal otoliths were obtained from 1400 hapuku collected from waters off New Zealand, from 1979 to 1995. Many otoliths were collected during studies by Johnston (1983) and Roberts (1986) and made available to us. Since then, additional otoliths have been collected by us during research trawl surveys and sampling trips aboard commercial line vessels, as well as by Ministry of Fisheries scientific observers aboard commercial line and trawl vessels.

Most otoliths were accompanied by information on fish total length (TL, to the centimeter below actual length) and sex. Three subsamples of these otoliths were selected for analysis. The first comprised 44 otoliths collected from five sites between Three Kings Islands and Great Barrier Island (Fig. 2) (hereafter called the "northern" sample). The second consisted of 178 otoliths collected from Cook Strait and Kaikoura (Fig. 2; "central" sample) and the third consisted of 28 otoliths from large hapuku collected from other sites throughout New Zealand ("miscellaneous" sample), selected to boost the number of old fish in the data set.

One otolith from each pair was viewed under transmitted polarized light, and the straightest dorsonuclear ridge was marked with a pen to guide the saw for sectioning. Each otolith was then embedded in a block of clear epoxy resin and sectioned transversely through the core at a thickness of 650 µm by using a dual-blade high-speed diamond saw. One face of the section was polished with carborundum paper and glued on to a microscope slide with thermoplastic cement. The opposite face was then ground and polished to a final thickness of 200–350 µm, depending on the clarity of the otolith bands when viewed under both reflected and transmitted light.

Opaque otolith bands were counted under transmitted light in the dorsal part of each section by two readers. Both readers carried out an initial training exercise by making counts on a subsample of the sections, while knowing the collection details of each fish (TL, sex, and site), and then discussed their results. Subsequent counts were carried out "blind"; i.e. the readers did not know the size, sex, or collection site of the hapuku. Reader 1 counted all sections once (R_1) and reader 2 counted all sections twice, the two counts being separated by two months ($R_{2,1}$ and $R_{2,2}$). The readability of sections was scored on a scale from 1 (unreadable) to 5 (exceptionally clear).

Otolith band counts were assessed for ageing bias and precision (between readers, and between read-

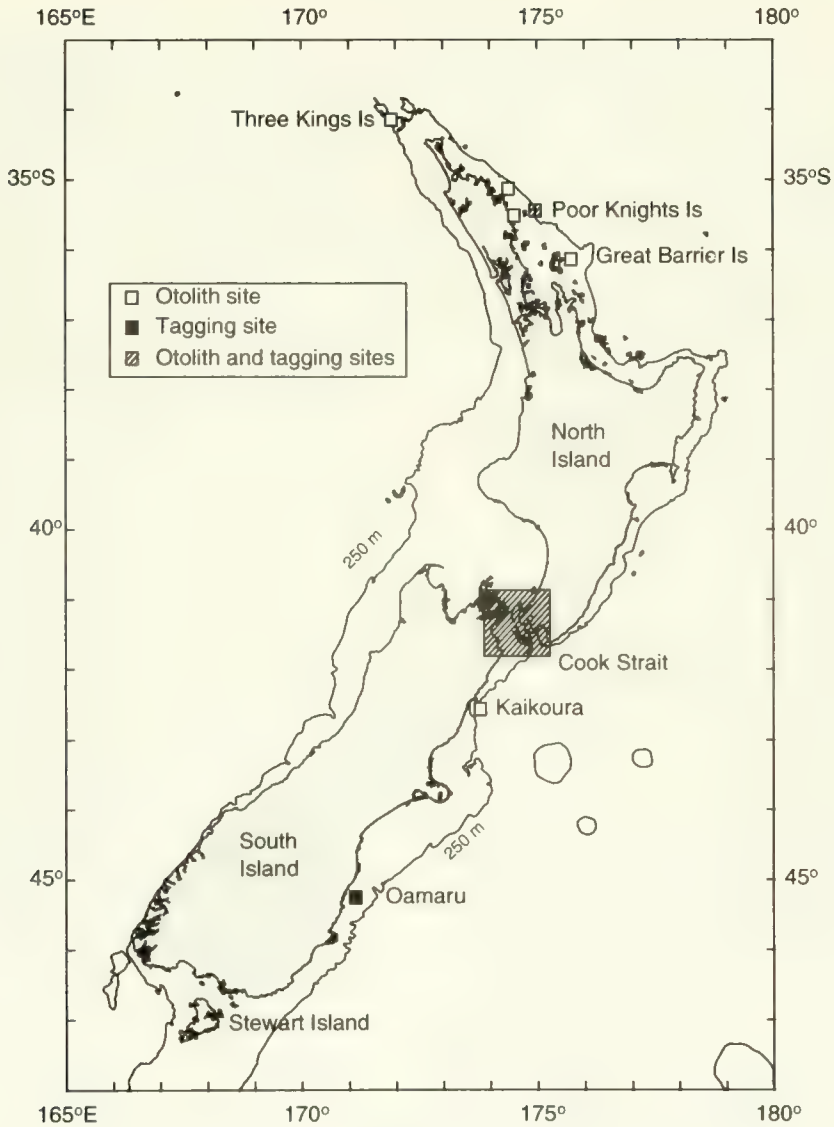

Figure 2

Hapuku otolith collection sites and tag-release sites.

ings by reader 2) by using age-bias plots and plots of the coefficient of variation (CV) against age, as recommended by Campana et al. (1995). These two plots show the means (and their standard errors), and the CVs, respectively, of the band counts made by reader x for each "age" as determined by reader y. For example, for all the hapuku that were judged by reader y to have 10 bands, the mean, standard error, and CV were calculated from the band counts made by reader x for the same fish, and plotted at age 10 on the x-axis. Age estimates made by reader 2 on the second reading ($R_{2,2}$) were selected as a baseline against which to compare other estimates because it was anticipated that the experience gained during the first reading would produce more reliable age estimates during the second reading.

Validation of the annual formation of otolith bands was attempted by marginal increment analysis and oxytetracycline injection. The marginal composition of 76 otoliths from northern and central hapuku, aged 3–8 years, was graded as opaque, narrow hyaline, or wide hyaline. The classification of hyaline zones as narrow or wide was based on a comparison of the marginal zone width with the width of the preceding hyaline zone. A qualitative classification was used because the presence of split opaque bands made it difficult to measure the marginal increment. The data were grouped into two-month intervals because not all months were sampled and because sample sizes were small.

Thirty-nine hapuku were tagged (see "Tag-recapture" section), injected intramuscularly with oxytet-

racycline hydrochloride (OTC), and released at the Poor Knights Islands (Fig. 2). Two OTC brands and dosage rates were used: 27 fish were injected with terramycin at a dosage rate of 80 mg/kg; and 12 were injected with engemycin at 35 mg/kg. Five OTC-injected fish were recaptured and their otoliths removed. One otolith from each pair was sectioned as described above and viewed under transmitted white light and reflected UV light. The composition of the otolith (number of opaque or hyaline bands) outside the OTC mark was determined, and the amount of new otolith material laid down along the dorsonuclear axis was measured.

Growth curves were fitted to the length-at-age data bu using the von Bertalanffy growth model:

$$L_t = L_\infty\left(1-e^{-K|t-t_0|}\right),$$

where L_t = the expected length at age t years;
L_∞ = the asymptotic maximum length;
K = the von Bertalanffy growth constant; and
t_0 = the theoretical age at zero length.

Length-frequency distributions

Hapuku length-frequency distributions were obtained from a series of four bottom trawl surveys conducted from the research vessel *Tangaroa* (towing a 60-mm mesh codend) off Southland (the southern coast of South Island and the Stewart Island shelf between latitudes 46–49°S). The surveys were carried out annually in February and March, 1993–96, and covered a depth range of 30–600 m. Further details of the surveys are provided in the studies of Hurst and Bagley (1994) and Bagley and Hurst (1995, 1996a, 1996b).

Von Bertalanffy growth curves were fitted to the four length-frequency distributions by using the MULTIFAN model (Fournier et al., 1990). This model analyses multiple length-frequency distributions simultaneously and uses a maximum likelihood method to estimate the number of age classes represented by the data, the proportions of fish in each age class, and the von Bertalanffy growth parameters L_∞ and K. The main assumptions of the MULTIFAN model are the following: 1) the lengths of the fish in each age class are normally distributed around their mean length; 2) the mean lengths-at-age lie on or near a von Bertalanffy growth curve; and 3) the standard deviations of the actual lengths about the mean length-at-age are a simple function of the mean length-at-age (Fournier et al., 1990).

The growth parameters were estimated by conducting a systematic search across a parameter space of plausible K values (0.005–0.30) and age classes (6–15). It is possible to constrain the MULTIFAN search further by specifying initial estimates for the mean length-at-age, and the range of the mean length, for one or more age classes (Fournier et al., 1990). However, this is not necessary when the length distributions contain adequate modal structure; therefore such constraints were not used in this study.

For each of the identified age classes, MULTIFAN also estimates the ratio of the last to first length standard deviations (S_R) and the geometric mean of the first and last standard deviations (S_A). The MULTIFAN model was fitted for two different growth hypotheses: 1) constant length standard deviation for all age classes (fitted by setting S_R=1 and estimating S_A); and 2) variable length standard deviation across age classes (fitted by estimating both S_A and S_R). Because all four trawl surveys were conducted at the same time of year, the data contain no information on seasonal variability of growth, and no seasonal parameters were fitted.

Each combination of K and the number of age classes constituted a model fit. The constant standard deviation hypothesis was fitted to the data first, followed by the addition of the parameter for variable standard deviation. For each combination of K, number of age classes, and growth hypothesis, the maximum log-likelihood (λ) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the increase in λ is distributed as a χ^2 distribution with degrees of freedom equal to the number of additional parameters. Following Fournier et al. (1990), a significance level of 0.10 was used for testing whether there was any gain in introducing an additional age class in the length-frequency analyses. The test for improvement resulting from the addition of the parameter for variable standard deviation was carried out with a significance level of 0.05.

The von Bertalanffy growth parameter t_0 was estimated from the equation

$$t_0 = t_1 - a_1,$$

where a_1 = the age estimated by MULTIFAN (in years since zero length) of the youngest age class at the time it first appeared in the length-frequency samples; and
t_1 = the time elapsed in years between the theoretical birthday and the first appearance of the youngest year class in the samples.

The theoretical birthday was defined as 1 September based on observations of prespawning fish in June–August and postspawning fish in October–December (Johnston, 1983; Roberts, 1986).

Tag recapture

1623 hapuku were tagged at three main sites: Poor Knights Islands (July 1987–August 1989, n=106), Cook Strait (August 1979–June 1984, n=599) and Oamaru (March 1988–April 1990, n=918) (Fig. 2). Fish were caught by longline or drop (dahn) line in depths less than 160 m. Only lively fish without everted stomachs or bulging eyes were tagged. Distended swimbladders were vented by means of a hollow needle inserted through the wall of the body cavity. Hapuku were measured (TL), tagged with a loop, dart, or spaghetti tag, and released. Oamaru hapuku were double tagged with both a loop and a dart tag. Loop and spaghetti tags were inserted through the muscle just anterior to the dorsal fin and clipped or tied together, and dart tags were inserted into the muscle directly below the first dorsal-fin ray. Each tag was printed with a serial number, a return address and notice of a reward. Recapture data and most measurements of recaptured hapuku were provided to the Ministry of Agriculture and Fisheries by the fishermen who caught them, but occasionally whole fish were returned for measurement.

Von Bertalanffy growth estimates were obtained from the tagging data by using the maximum likelihood method and the computer program GROTAG (Francis, 1988). GROTAG also estimates g_α and g_β, the mean annual growth of fish of lengths α and β respectively. The reference lengths α and β were chosen to lie within the range of lengths of tagged hapuku. Francis (1988) showed that these parameters describe the growth information in tagging data better than the more conventional von Bertalanffy growth parameters L_∞ and K do. The expected length increment, ΔL, for a fish of initial length L_1 at liberty for time ΔT is given by

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1 \right] \left[1 - \left(1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T} \right].$$

Also estimated were m and s (the mean and standard deviation of the measurement error), v (the coefficient of variation of growth variability), and p (the proportion of outliers) (Francis, 1988). Preliminary GROTAG fits suggested that the von Bertalanffy growth model was not appropriate for tagged hapuku; therefore a linear GROTAG function with only one growth parameter (g_α) was fitted to the data. A seasonally varying growth function was also tested. Differences in growth rate between the two sexes in Cook Strait (the sex of recaptured fish was not determined for the other two areas) and among the three tagging areas were also investigated.

The approach used was to fit a simple GROTAG model with few parameters to the data. The complexity of the model was then gradually increased by introducing additional parameters (for example, parameters to allow for seasonal variation in growth). At each stage, new parameter estimates were made and likelihood ratio tests for significant improvement in model fit were carried out as described above for MULTIFAN models. A significance level of 0.05 was used for testing whether there was any gain from introducing additional parameters.

Results

Otolith ageing

Otolith structure The otoliths of the hapuku we examined had an opaque core (dark in transmitted light) and an opaque line that radiated along the dorsoventral axis (Fig. 3). The line was usually split by 1–3 hyaline bands (light in transmitted light). The sulcus was also mostly opaque. The remainder of the otolith consisted of alternating opaque and hyaline bands. In young fish, the hyaline bands were wider than the opaque bands, but difference in width declined in older fish. Opaque bands usually consisted of multiple, fine, wavy opaque and hyaline zones (Figs. 3 and 4A). The demarcation between each compound opaque band and the adjacent hyaline bands was often indistinct, making the bands difficult to count. The banding pattern was usually clearest in the dorsal half of transverse otolith sections. We used counts of the compound opaque bands as age estimates.

Five otolith sections were considered unreadable, and a further four otoliths were lost or damaged during preparation. Of the remaining 241 otoliths, 78% were scored as poor or moderate (readability 2 or 3); only 22% were good or exceptionally clear (readability 4 or 5).

Validation Otolith marginal state was difficult to assess because of the presence of split opaque rings. There was no apparent seasonal cycle in marginal composition, and sample sizes in most two-month periods were inadequate to provide good estimates of the percentage of the population with opaque margins (Jan–Feb percent opaque=50.0, n=14; Mar–Apr 37.5, 8; May–Jun 36.4, 33; Jul–Aug 42.9, 7; Sep–Oct 50.0, 10; Nov–Dec 25.0, 4). The same conclusion was reached for the central data alone (n=50).

Five OTC-injected hapuku were recaptured after 0.20–2.66 years at liberty (Table 1). All had distinct, bright OTC bands when viewed under UV light (Fig. 4B). There was no apparent relation between OTC

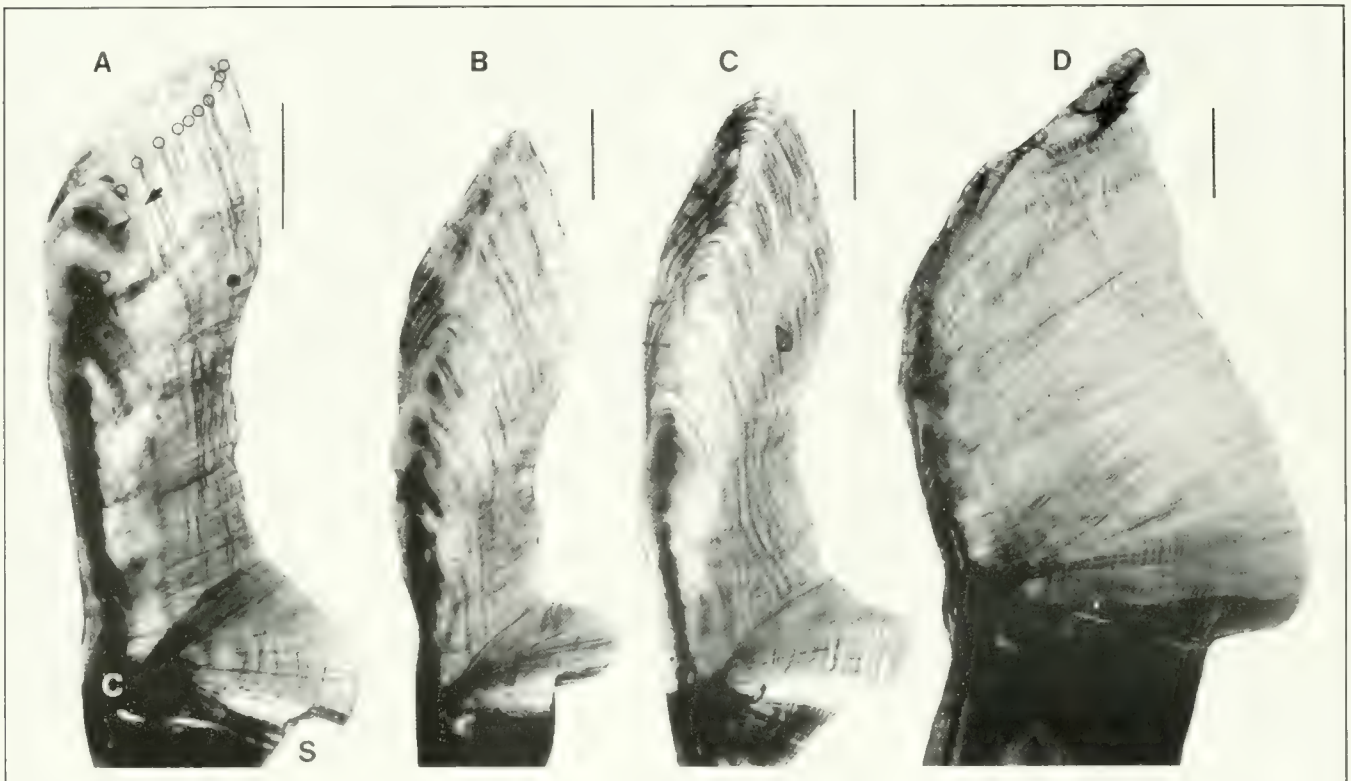

Figure 3

Photomicrographs (transmitted white light) of the dorsal halves of transverse sections of hapuku otoliths from (**A**) an 85-cm female, northern, readability 3, estimated age (mean of R_1, $R_{2.1}$ and $R_{2.2}$) 11.7 years; C = core, S = sulcus, arrows indicate a compound opaque band, circles indicate opaque bands; (**B**) an 87-cm female, Cook Strait, readability 4, age 14.7 years; (**C**) a 106-cm male, Cook Strait, readability 4, age 19.0 years; (**D**) an 121-cm male, Kaikoura, readability 5, age 45.7 years. Scale bars = 1 mm.

Table 1

Details of recaptured hapuku that were tagged and injected with oxytetracycline (OTC). M = male, T = terramycin, E = engemycin, — = not determined. Increment width is the amount of postinjection otolith material deposited along the dorsonuclear otolith axis. Increment pattern is the type of material (O=opaque, H=hyaline) laid down between the OTC mark (m) and the otolith margin. An "I" subscript indicates an incomplete band, and a question mark indicates uncertainty in determining the composition of the otolith margin.

Tag number	Length at tagging (cm)	Length at recapture (cm)	Sex	OTC brand	Date tagged	Date recaptured	Years at liberty	Increment width (mm)	Increment pattern
SGO306	89	104	M	T	20 Oct 87	19 June 90	2.66	0.61	mO_IHOHOH
SGO322	85	87	M	T	8 Jul 88	21 Dec 88	0.45	0.08	mO_IH_I
SGO328	55	55	—	E	27 Oct 88	10 Mar 89	0.37	0.16	mO_IH_I
SGO329	73	77	—	E	2 Dec 88	12 May 89	0.44	0.05	mHO_I?
SGO340	68	65	—	E	2 Jul 89	14 Sep 89	0.20	0.01	mO_IH_I?

brand (terramycin or engemycin) or dosage and the width or intensity of the OTC mark. Four hapuku injected with OTC in July–October showed an OTC mark that fell within an opaque band, indicating that opaque bands are formed in the austral winter–spring. The remaining fish was injected in December and had an OTC mark at the distal edge of an opaque band, indicating that hyaline band formation begins in spring–summer.

The OTC results from all five hapuku are consistent with the deposition of one hyaline-opaque band pair on the otolith each year. The hapuku that had

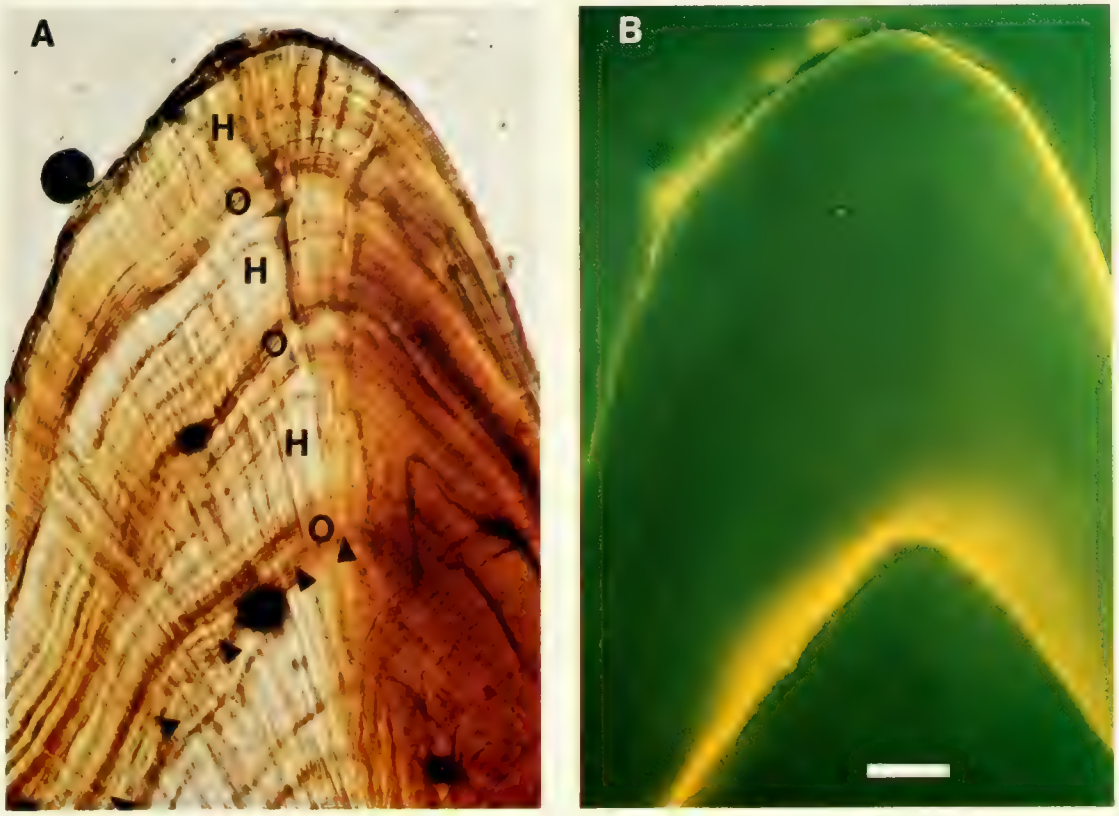

Figure 4

Photomicrographs of the dorsal end of a transverse section from a hapuku otolith illuminated by (**A**) transmitted white light, and (**B**) reflected UV light. The hapuku had been tagged, injected with oxytetracycline, and recaptured after 2.66 years at liberty (see Table 1, tag number SGO306, for further details). Arrowheads indicate the position of the inner edge of the oxytetracycline mark, which lies within an opaque band. Outside that band are three hyaline (H) and two opaque (O) bands. Scale bar = 0.1 mm.

been at liberty for the shortest time (SGO340, 0.20 years) had the OTC mark near the margin (postinjection increment width along the dorsal axis=0.01 mm) (Table 1). Three hapuku with intermediate periods at liberty (0.37–0.45 years) had moderate postinjection otolith increments of 0.05–0.16 mm. SGO328, which was the smallest of the three hapuku at tagging, had the largest increment. SGO322 and SGO328 each had an incomplete opaque band and an incomplete hyaline band outside the OTC mark. SGO329 had a complete hyaline band and possibly an opaque band beginning to form at the margin near the dorsal tip of the otolith. A hapuku that had been at liberty for 2.66 years (SGO306) had a wide postinjection increment (0.61 mm) consisting of a partial opaque band followed by three hyaline and two opaque bands (Fig. 4; Table 1).

Age estimates and growth rates $R_{2.1}$ and $R_{2.2}$ were strongly positively correlated (coefficient of multiple determination [R^2]=94.6), although they differed markedly for some individuals (Fig. 5A). Some of the larger differences were for otoliths that were judged difficult to count (readability 2), but large differences were also found for clearer otoliths (readability 3–5). $R_{2.1}$ tended to be higher than $R_{2.2}$ for fish aged 3–18 years in $R_{2.2}$ (mean difference=1.0 years) (Fig. 6A). Sample sizes were small for hapuku older than 18, but it appears that the same bias occurred for them.

Age estimates made by both readers (R_1 and $R_{2.2}$) were also highly correlated (R^2=92.4) but there were some substantial differences (Fig. 5B). There was no apparent bias between the two sets of estimates for hapuku aged 3–12 in $R_{2.2}$, but there was a slight tendency for $R_{2.2}$ to exceed R_1 over the range 13–18 years (Fig. 6B).

Ageing precision was low and variable, both within and between readers, for hapuku aged 3–18 years (Fig. 7). The CV of the age estimates was slightly lower between the two readings of reader 2 ($R_{2.1}$ ver-

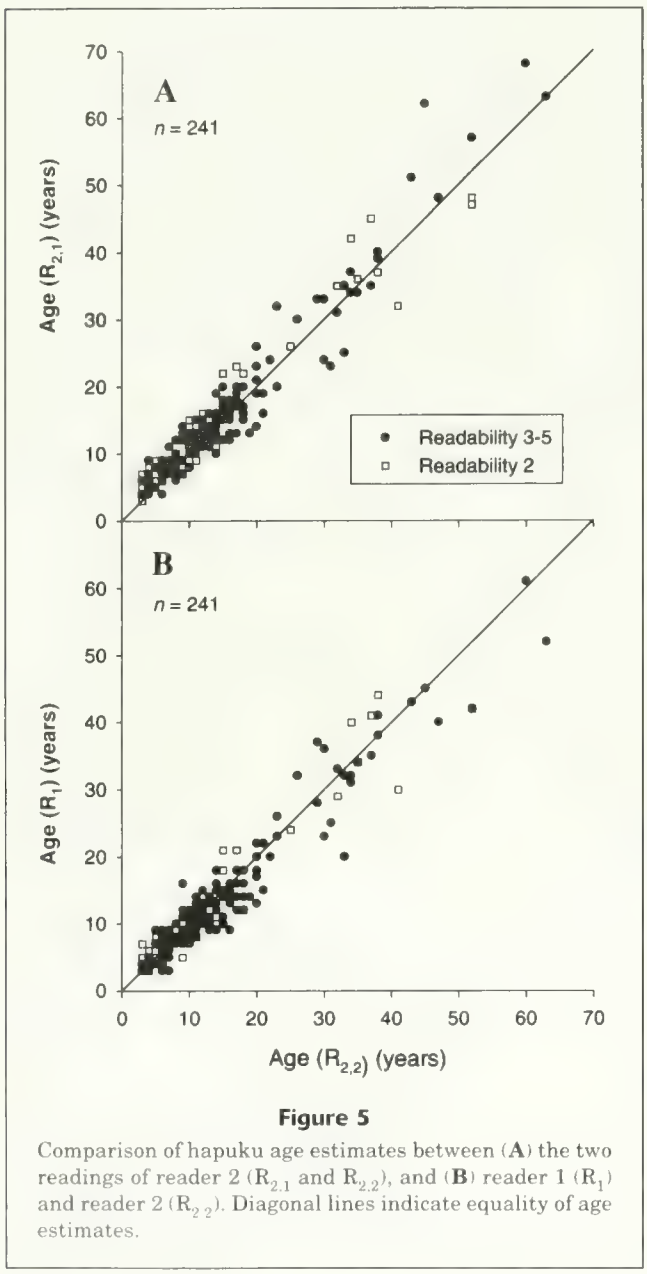

Figure 5

Comparison of hapuku age estimates between (**A**) the two readings of reader 2 ($R_{2,1}$ and $R_{2,2}$), and (**B**) reader 1 (R_1) and reader 2 ($R_{2,2}$). Diagonal lines indicate equality of age estimates.

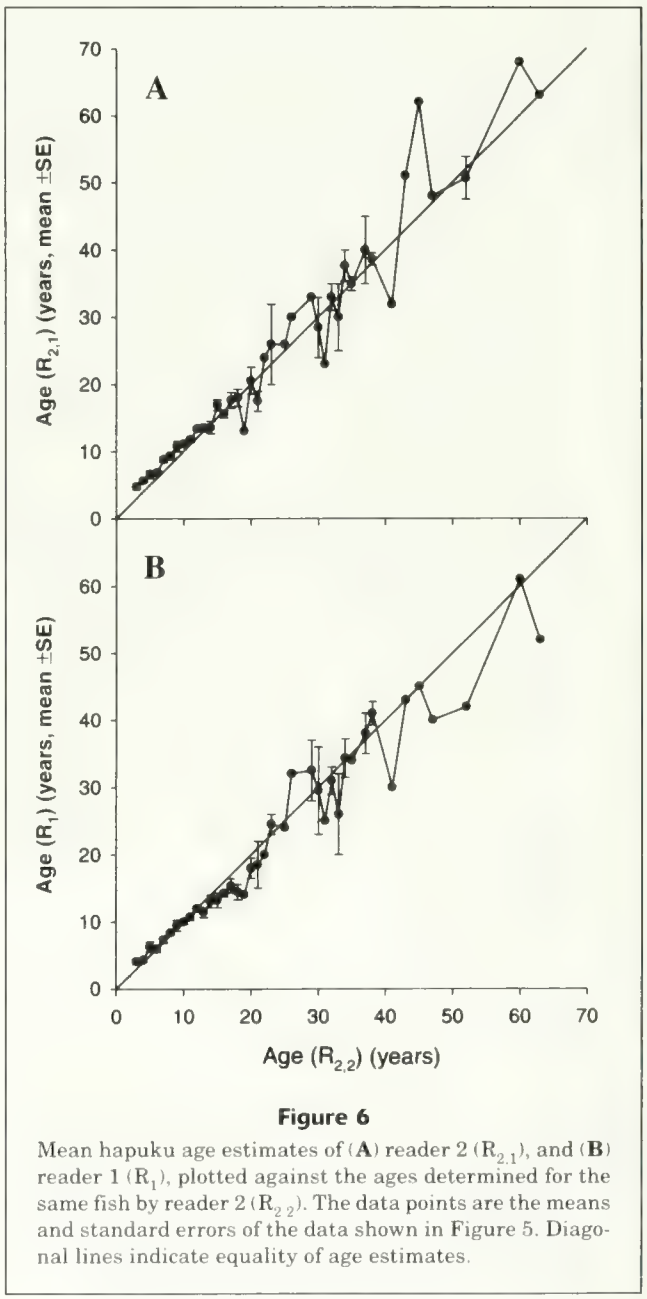

Figure 6

Mean hapuku age estimates of (**A**) reader 2 ($R_{2,1}$), and (**B**) reader 1 (R_1), plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the means and standard errors of the data shown in Figure 5. Diagonal lines indicate equality of age estimates.

sus $R_{2,2}$) (mean=18.0%, range=10.1–26.1%) than between readers (R_1 versus $R_{2,2}$) (mean=21.3%, range=12.6–31.4%). The CV declined slightly with increasing age for both the within- and between-reader comparisons.

The main differences between counts arose from 1) different band counts near the otolith core (potential age difference=1–3 years), 2) different band counts in an unclear central zone around bands 4–8 (several years), and 3) classification of the composition of the otolith margin as opaque or hyaline (one year).

The greatest estimated ages (mean of R_1, $R_{2,1}$ and $R_{2,2}$) were 50.3, 50.7, 59.3, and 63.0 years, but few fish were found to be more than 20 years old (Fig. 5). The youngest hapuku were 3 years old. The von Bertalanffy growth curve fitted to R_1 data differed little from that fitted to $R_{2,2}$ data (Fig. 8A; Table 2). Females grew faster than males, but the difference was slight, and the overlap of data points was substantial (Fig. 8B; Table 2). The largest male was 134 cm, the largest female 147 cm (with three females longer than 140 cm).

Growth curves fitted separately to the northern and central data were very similar (Table 2). Inspection of the residuals from the central curve again

Table 2

Von Bertalanffy growth curve parameters based on hapuku length-at-age and length-frequency data. Standard error estimates for the MULTIFAN parameters are considered unreliable and are not shown. SE = standard error, R_1 = reader 1, $R_{2,2}$ = reading 2 of reader 2, M = male, F = female.

Sample	Otolith reading	Sex	Sample size	$L_\infty \pm$ SE (cm)	$K \pm$ SE	$t_0 \pm$ SE (years)
Length-at-age data (otoliths)						
All	$R_{2,2}$	M + F	241	131.7 ± 3.2	0.0666 ± 0.0059	−4.63 ± 0.72
All	R_1	M + F	241	131.0 ± 2.3	0.0785 ± 0.0052	−2.96 ± 0.48
All	$R_{2,2}$	M	105	129.2 ± 5.4	0.0618 ± 0.0095	−5.75 ± 1.32
All	$R_{2,2}$	F	110	133.2 ± 4.2	0.0698 ± 0.0084	−4.30 ± 1.01
Northern	$R_{2,2}$	M + F	44	124.0 ± 9.8	0.0699 ± 0.0193	−4.51 ± 1.96
Central	$R_{2,2}$	M + F	172	122.6 ± 5.3	0.0794 ± 0.0117	−4.06 ± 0.89
Length-frequency data (MULTIFAN)						
Southern	—	M + F	1,471	549.2	0.0090	−8.02

suggested that females grew slightly faster than males, although there was strong overlap in the ranges (males: mean residual=−1.8 cm, SD=8.6, n=90; females: mean=1.6, SD=7.8, n=82). All growth curves had strongly negative values for t_0 (Table 2).

Length-frequency distributions

Hapuku from the four southern trawl surveys generally were less than 85 cm long (Fig. 9), and because 50% maturity occurs at about 85 cm and 88 cm for males and females, respectively (Johnston, 1983), these would have been immature. The smallest hapuku was 41 cm long, but few fish were less than 50 cm. This reflects the pattern seen in the entire New Zealand research trawl database which contains length measurements for 5841 hapuku: the smallest hapuku was 40 cm, and only 55 were less than 50 cm long.

The best-fit MULTIFAN model consisted of constant length standard deviation with 11 age classes (see Table 2 for growth parameters). The estimated time elapsed between the theoretical birthday and the first appearance of juvenile hapuku in the length-frequency samples (t_1) (based on an estimated minimum age at first capture from otolith ageing of 3 years, plus 0.5 years elapsed between the theoretical birthday [1 September] and the sampling date midpoint [1 March]) was 3.5 years. The age in years since zero length of the youngest age class at the time it first appeared in the length-frequency samples (a_1) was estimated by MULTIFAN to be 11.52 years, producing a t_0 estimate of −8.02 years. The standard error estimates provided by MULTIFAN for the growth parameters are not presented in Table 2 because they tended to be unrealistically small (Francis and Francis, 1992).

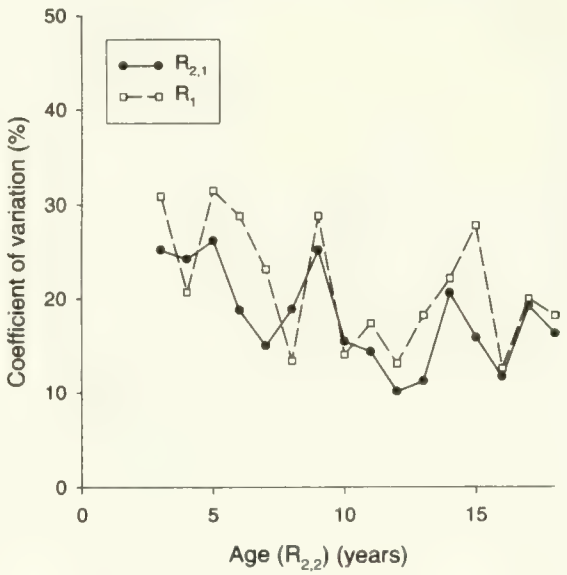

Figure 7

Precision of hapuku age estimates of reader 2 ($R_{2,1}$) and reader 1 (R_1) plotted against the ages determined for the same fish by reader 2 ($R_{2,2}$). The data points are the coefficients of variation of the data shown in Figure 4.

The growth curve resulting from the best MULTIFAN fit to the length-frequency data was nearly linear over the range of the data (Fig. 10). The curve was truncated at 14.5 years, which is the maximum age covered by the data (calculated as the sum of the number of age classes detected by MULTIFAN [11] and the estimated age at first recruitment to the samples [3.5 years]). The MULTIFAN curve should not be extrapolated beyond this point because the

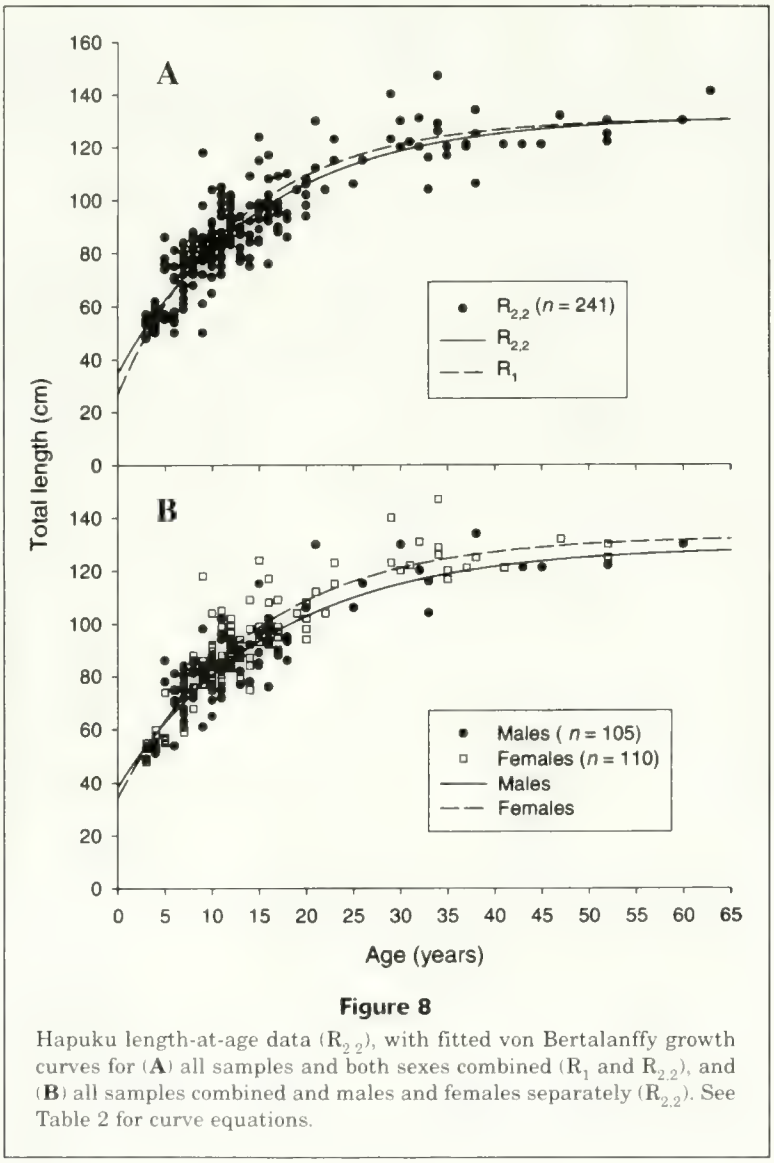

Figure 8

Hapuku length-at-age data ($R_{2,2}$), with fitted von Bertalanffy growth curves for (**A**) all samples and both sexes combined (R_1 and $R_{2,2}$), and (**B**) all samples combined and males and females separately ($R_{2,2}$). See Table 2 for curve equations.

length-frequency data represent only small, immature hapuku. Over the age range 0–12 years, the MULTIFAN growth curve was very similar to growth curves based on otolith ages (Fig. 10).

Tag recapture

One tagged hapuku was recaptured, released with a new tag, and recaptured a second time (Johnston, 1992). It grew from 73 cm to 83 cm during its first 800 days at liberty and from 83 cm to 96 cm during its second 829 days at liberty. This fish was entered into the growth data set three times: once for each of the two periods at liberty and once for the combined period at liberty. All other hapuku used in the growth analysis were recaptured only once.

One hundred and forty four recaptured hapuku had sufficient information (lengths at tagging and recapture, days at liberty) to be used in the growth analysis. Most of these hapuku were between 50 and 90 cm long at tagging (Fig. 11) and would have been immature. The GROTAG reference lengths α and β were set at 55 cm and 85 cm respectively. Periods at liberty ranged from 9 to 3708 days (0–10.2 years), but most fish were at liberty for less than four years (Fig. 12).

Initial GROTAG model fits identified six fish as outliers (fish having absolute standardized residuals greater than 3.0). Five of these fish had negative growth increments of 3–27 cm, and one had a positive increment of 24 cm after 347 days at liberty. These outliers probably resulted from measurement

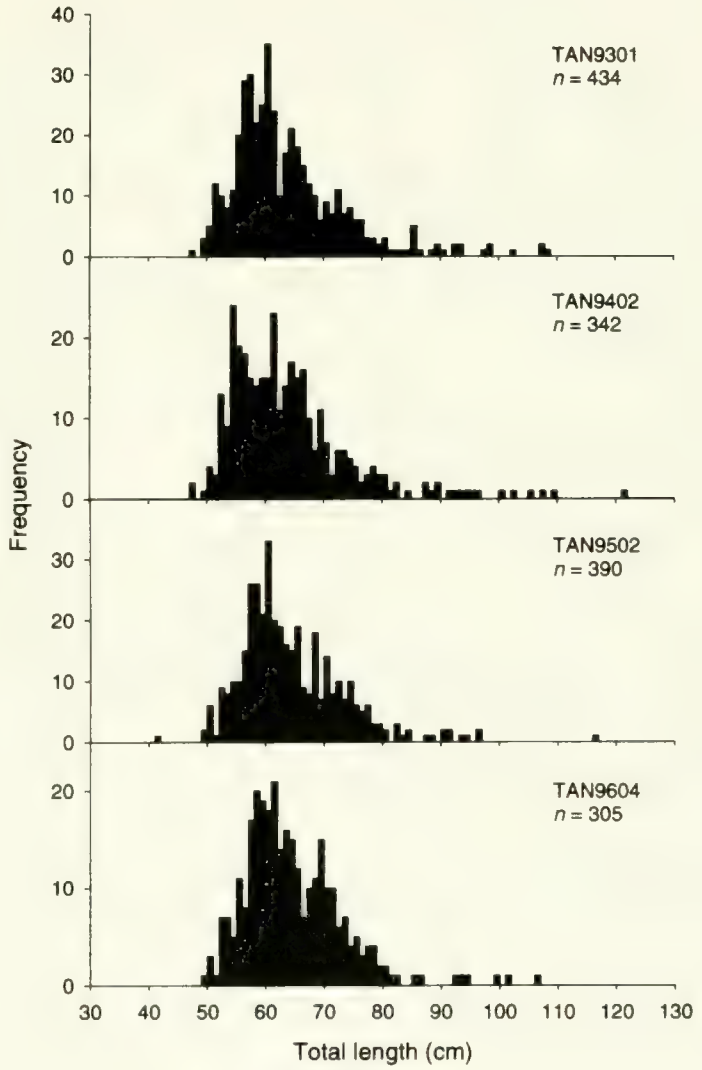

Figure 9

Hapuku length-frequency distributions (both sexes combined) obtained from four *Tangaroa* trawl surveys off Southland in February–March 1993–1996. *n* = sample size.

errors and were deleted from the data set, leaving 138 fish.

A simple linear model, with a single growth-rate parameter, produced an estimated growth rate of 4.26 cm/yr (Table 3, model 1). A model with two growth-rate parameters produced no improvement in fit (Table 3, model 2). The addition of parameters for outlier contamination, measurement bias, and seasonal growth did not significantly improve the log-likelihood (Table 3, models 3–5), nor did subdivision of the data into three geographical areas (Table 3, model 6). For the Cook Strait data subset, inclusion of separate growth parameters for male and female hapuku did not significantly improve the model fit (Table 4). However, sample sizes were small, statistical power was low, and only large differences could have been detected.

Therefore the best GROTAG model (Table 3; model 1) consisted of simple linear growth over the length range 55–85 cm. It had no apparent pattern or trend in the residuals. GROTAG was then run in simulation mode (Francis, 1988) by using parameter estimates from model 1 to determine the accuracy and precision of the growth-rate estimate. The mean annual growth rate was estimated to be 4.25 cm/yr with a standard error of 0.017 cm/yr.

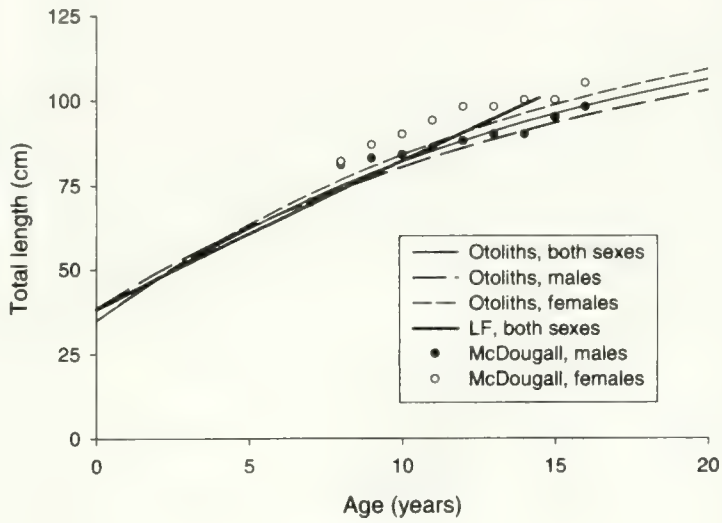

Figure 10

Comparison of growth curves derived from length-at-age data ($R_{2.2}$, otoliths), and MULTIFAN analysis of length-frequency data (LF). Also shown are the mean lengths-at-age reported by McDougall (1975) for hapuku collected in Cook Strait.

Table 3

Parameter estimates from GROTAG growth models for hapuku from all tagging sites (n=138). Seasonal phase is given in years since 1 January. SD = standard deviation; — = parameter not estimated. Models 1–5 are for Poor Knights Islands, Cook Strait, and Oamaru, data combined; model 6 estimated g_{55} separately for the three areas.

		All areas combined					Areas separate
Parameter		1	2	3	4	5	6
Log likelihood	2λ	697.80	697.42	697.80	697.80	694.30	695.85
Mean growth rates	g_{55} (cm/yr)	4.26	4.01	4.24	4.25	4.25	4.1–5.0
	g_{55} (cm/yr)	—	4.38	—	—	—	—
Growth variability	t	0.38	0.39	0.39	0.39	0.39	0.39
SD measurement error	s (cm)	1.55	1.54	1.55	1.55	1.51	1.51
Measurement bias	m (cm)	—	—	—	0.05	—	—
Outlier contamination	p	—	—	0.00	—	—	—
Amplitude	u	—	—	—	—	0.53	—
Phase	w (yr)	—	—	—	—	0.15	—

Discussion

Hapuku otoliths frequently had split opaque bands and were difficult to age. This led to reduced counting precision and, for some age groups, to a small between- and within-reader ageing bias. Our use of marginal increment analysis to validate hapuku otolith ageing was inconclusive. We attribute this to the compound nature of the opaque bands and to the resulting difficulty in determining whether the material being deposited at the margin was opaque or hyaline.

The results of the OTC injection experiment were consistent with the deposition of one opaque and one hyaline band per year. This does not constitute full validation of the otolith ageing technique because the

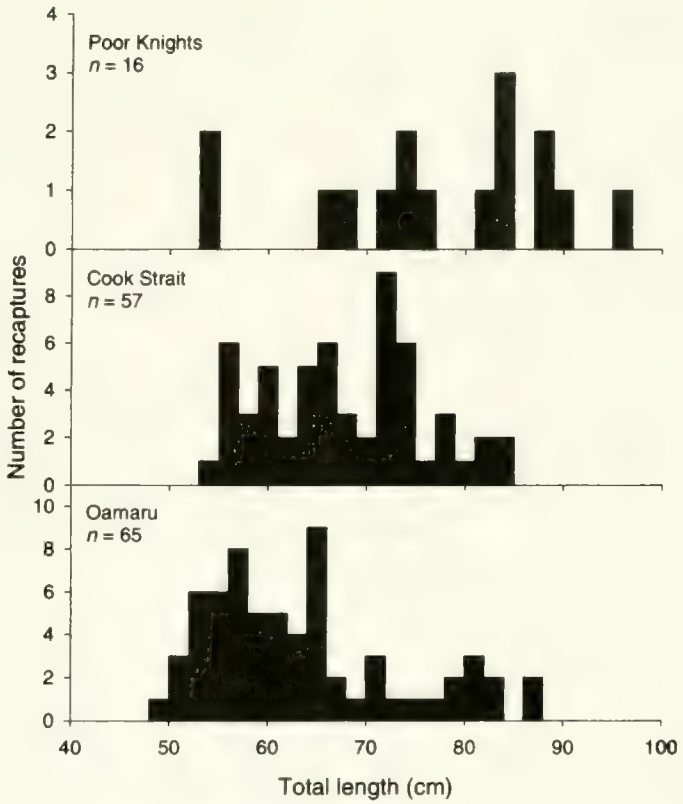

Figure 11

Length-frequency distributions (at tagging) of tagged and recaptured hapuku used in the GROTAG analysis of growth rates. n = sample size.

experiment included only five hapuku, only one of which was at liberty for more than one year. Furthermore, all five fish would have been immature or just maturing at the time of injection. Further validation is required, especially for older, mature hapuku.

An independently derived von Bertalanffy growth curve (based on MULTIFAN analysis of length-frequency data) agreed well with the otolith-based length-at-age curves over the age range 0–12 years but indicated faster growth rates for hapuku aged 12–14.5 years (Fig. 10; Table 5). Our previous experience has shown that MULTIFAN growth curves are generally reliable for younger age classes, which often exhibit discernible length modes, but are not reliable for older age classes, which usually lack any modal length structure. This is because MULTIFAN underestimates the number of older age classes present in the data and consequently overestimates the length-at-age of the older age classes (Francis and Francis, 1992; Francis, 1997). Therefore, the discrepancy between the MULTIFAN and length-at-age curves for the older age classes in Fig. 10 probably arises from bias in the former. This interpretation is supported by the near-linearity of the MULTIFAN growth curve and the implausible MULTIFAN growth parameters, especially L_∞ (Table 2).

Table 4

Parameter estimates from GROTAG growth models for hapuku from Cook Strait (n=43). SD = standard deviation;— = parameter not estimated.

Parameter		Both sexes	Sexes separate M	F
Log likelihood	2λ	240.44	240.26	
Mean growth rates	g_{55} (cm/yr)	4.53	4.44	4.64
	$g_{\infty 5}$ (cm/yr)	—	—	
Growth variability	v	0.27	0.27	
SD measurement error	s (cm)	1.94	1.99	

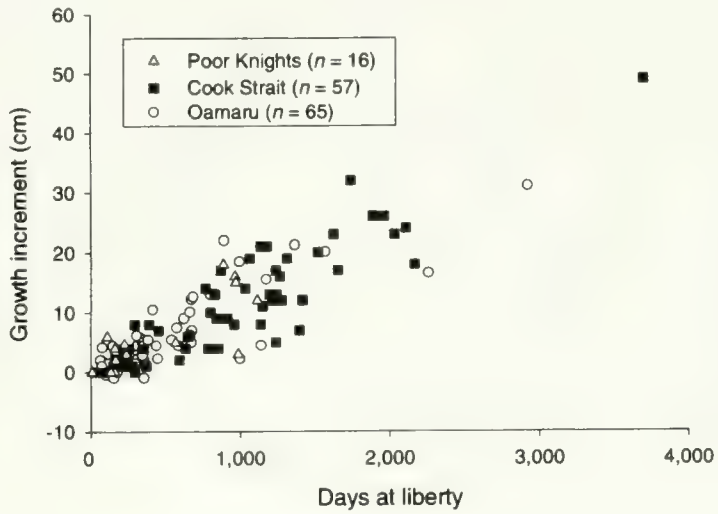

Figure 12

Relationship between growth increment and period at liberty for tagged hapuku. n = sample size.

Table 5

Comparison of hapuku annual growth increments at two reference lengths (55 cm and 85 cm) based on length-at-age ($R_{2,2}$), length-frequency, and tag-recapture data.

Total length (cm)	Annual growth increment (cm)		
	Length-at-age	Length-frequency	Tag-recapture
55	4.94	4.40	4.25
85	3.00	4.15	4.25

The best GROTAG model fit estimated the mean annual growth rate to be 4.25 cm/yr over the length range 55–85 cm. That estimate falls between the length-at-age estimates of annual growth for 55-cm and 85-cm hapuku (Table 5). A nonlinear growth model was not significantly better than the linear model, probably because of the narrow length range of the tag-recapture data, and the small sample size (n=138).

We conclude that the growth curves and growth rate estimates derived from length-frequency and tag-recapture data are consistent with those from otolith-based, length-at-age data for the length and age ranges over which the data overlap. In conjunction with the results of the OTC injection experiment, this agreement among growth-rate estimates provides strong support for our hypothesis that otolith band pairs are deposited annually in hapuku.

Our length-at-age growth curve for male hapuku is similar to that of McDougall (1975), who made band counts in broken and burnt otoliths from hapuku collected in Cook Strait (Fig. 10). However, McDougall reported a slightly faster growth rate for females (Fig. 10). It is not possible to determine whether the difference in female growth rates is real, or a result of McDougall's small sample size (n=72). McDougall's largest hapuku was 120 cm and his oldest fish was 26 years.

A study of hapuku growth at Juan Fernández Island, based on scale annuli, reported much faster growth rates and a maximum age of only 12 years (Pavez and Oyarzún, 1985). Scale rings are typically crowded to the point of being unresolvable in hapuku older than 8 years (McDougall, 1975); it is likely therefore that the ages of Pavez and Oyarzún's larger fish were underestimated.

Lack of precision and reader bias mean that otolith ageing is unlikely to be useful when accurate hapuku ages are required (e.g. in the estimation of year-class strength from an age-frequency distribution). However, the precision and accuracy problems experienced in this study had little effect on the shape of growth curves fitted to length-at-age data, and we believe that the growth parameters reported here are relatively robust.

The large negative t_0 values for all growth curves indicate a lack of fit of the von Bertalanffy model to the data for small hapuku. This may result from one or more of the following: 1) lack of fish less than three

years old in our data; 2) underestimation of the ages of hapuku because of failure to recognize and count all the annual bands near the core; or 3) different growth rates of pelagic juveniles, and demersal juveniles and adults. Interestingly, Pavez and Oyarzún's (1985) scaled-based growth curves had t_0 values close to zero, and estimated ages at the length of settlement similar to ours (i.e. 38 cm at age 3 and 49 cm at age 4). Scale bands may therefore help to resolve problems experienced in interpreting otolith cores when ageing small hapuku.

Small juvenile hapuku pass through a pelagic stage in surface waters, usually associated with flotsam, and are rarely caught (Cormack, 1986; Michael, 1988; Roberts, 1996). At the end of the pelagic stage, they become demersal in depths of 50–600 m. Bottom trawl length-frequency data (Fig. 9; NIWA[2]) and bottom set-net and line records (Johnston, 1983; Roberts, 1989) indicate that most hapuku switch from a pelagic to demersal life style at around 50 cm, although hapuku as small as 40 cm have been caught by bottom trawl. A 35-cm hapuku reported caught in Wellington Harbour by Hector (1888) may have been a pelagic juvenile, but no details were given of habitat or fishing method. A small number of pelagic juveniles up to 67 cm long have been caught on surface longlines over 2000 m or more of water (Roberts, 1996; Scientific Observer Database[3]). These large pelagic juveniles may have become "stranded" in the pelagic environment after being carried over deep water by oceanic currents. Presumably they remain in surface waters until they encounter shallower depths, at which time they settle to the seabed.

Our best estimate of the age at which hapuku settle to a demersal habitat is 3–4 years, but our interpretation of the banding pattern near the otolith core was uncertain and somewhat subjective. Counts of possible daily increments in otolith sections also suggest settlement at about 3 years (Roberts, 1996), and a similar age range has been suggested by other studies (McDougall, 1975; Johnston, 1983). *Polyprion americanus* apparently settles at lengths greater than 45–55 cm and ages greater than 1–7 years (Sedberry et al., 1996).

The age at recruitment of hapuku to commercial trawl catches is likely to be the same as the age at settlement to the seabed. Although our research vessel samples were caught with a small mesh (60-mm) codend, hapuku longer than 50 cm are also retained by the larger mesh sizes used by commercial vessels (typically 100–125 mm) (Hurst and Bagley, 1997).

Previous studies have suggested that female hapuku grow larger and faster than male hapuku (McDougall, 1975; Roberts, 1986; 1989). Our results support those conclusions but also indicate that the differences in both maximum length and growth rate are small and, for most purposes, trivial. However, our ability to detect growth rate differences between the two sexes, and between sample sites, was limited by the low precision of our age estimates and the small sample sizes available for the GROTAG analysis.

Hapuku mature at about 85 and 88 cm, males and females, respectively (Johnston, 1983). Based on the length-at-age growth curves given in Table 2, age at maturity is estimated to be 10–13 years for both sexes.

The largest hapuku in our study was 147 cm TL, but they are known to reach 178 cm TL and 76 kg in weight (Roberts[4]). The longevity of hapuku cannot be precisely determined because of difficulties we experienced in estimating ages from otoliths, and because our samples mostly came from populations of hapuku that had been exploited for many years. Our study does suggest that hapuku live at least 50 years, possibly in excess of 60 years.

Acknowledgments

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An analysis of the possible utility of time–area closures to minimize billfish bycatch by U.S. pelagic longlines

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Abstract.—This study examined the relative rates of billfish bycatch and target species catch by areas (1°, 2°, and 5° latitude and longitude) and months in the catch data reported in mandatory log books kept by U.S. pelagic-longline fishermen in order to identify potential time–area strata that could reduce billfish bycatch. The 1986–91 mean percentages identified month–area strata with high percentages of sailfish and marlin bycatch and marlin only bycatch. The analyses indicated that the elimination of effort in cells selected according to percentages of billfish in the catch could have reduced the 1986–91 billfish bycatch by 50% and the target species from 13.9 to 19.2%, depending on the spatial resolution employed. The corresponding analysis of marlin only indicated a 50% reduction in marlin bycatch could have been attained and a 16.4–20.7% reduction in the target species catch. The time–area closures identified in the 1986–91 logbook data were applied to the data for 1992–95 and provided a test of the spatial and temporal stabilities of these results. For the evaluation of sailfish and marlin combined, the reductions in both billfish bycatch and target species catches averaged less than the predicted values, but in all cases billfish were selectively protected. For the evaluation of marlin only, the reduction of sailfish bycatch was less than the predicted amount and the reduction of the target species was slightly greater than the predicted value. The agreement between the predicted level of protection for billfish or marlin and the mean value for the 1992–95 test period increased with increasing size of the grid. At the 5°cell size, the mean reduction was 22.8% for the targeted species and 48.6% for marlin (compared with predicted values of 20.7 and 50% respectively). These results suggest that time and area restrictions on fishing could significantly reduce the bycatch of billfishes in the pelagic-longline fisheries without equivalent reductions in the catch of target species.

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The U.S. Fisheries Management Plan for Atlantic Billfishes (sailfish, blue and white marlin, and spearfish) reserves billfish stocks for recreational use; their commercial harvest by U.S. fishermen has been prohibited since the plan became effective in 1988 (SAFMC, 1988). The most recent stock assessment for billfishes found that, over the Atlantic as a whole, blue and white marlin stocks are seriously overfished (Anonymous, 1996). Their stocks were at about 21 and 24%, respectively, of the biomass needed to support maximum sustainable yield (MSY) at the beginning of 1996 (Anonymous, 1996). Fishing-induced mortality was estimated to be 3.19 times higher than that which would produce MSY for blue marlin, and 1.88 times higher than that which would produce MSY for white marlin. Most of the fishing mortality on these species is the result of bycatch in the pelagic-longline fisheries that target other species, particularly tuna and swordfish.

Many authors have promoted the concept of marine reserves (also called marine protected areas or MPAs) as management tools to enhance conservation of fishery resources (Bohnsack, 1994; Shackell and Wilson, 1995; Hutchings, 1995, 1996; Allison et al., 1998; Lauck et al., 1998). Closed areas have been used in many parts of the world to control bycatch mortality (Alverson et al., 1994). Hutchings (1996) noted that MPAs might have considerable merit in reducing bycatch when assessed against the effectiveness of other forms of regulatory control such as bycatch limitations and catch quotas. Often, however, the concept of marine reserves is restricted to closures of particular habitats or portions of habitats. Kenchington (1990) noted that such marine reserves would be of little use for species such as billfish that have both pelagic larvae and highly pelagic adults. Among other options for reducing bycatch, Alverson et al. (1994) observed that time–area control of fishing activity offers an opportunity to reduce unwanted bycatch. The main objective of employing time–area strategies is to take advantage of variation in the degree of co-occurrence between target and bycatch species (Murawski, 1992). The effectiveness of such controls obviously depends on the degree of overlap between the bycatch and the targeted species (Adlerstein and Trumble, 1992).

Cramer (1996) used logbook data on U.S. large pelagic fish (data that have been mandatory since October 1986) in order to evaluate the spatial distribution of the catch of undersized swordfish by the longline fishery in strata of 1° latitude and longitude by season and area. Her study evaluated the implications of removing time–area strata with high swordfish discard rates on the total catch of the longline fishery. The present study uses the same data set to evaluate the degree of

overlap between billfish bycatch and target species catch for the U.S. pelagic longline fishery and develops a method for selecting candidate time–area cells whose closure would selectively enhance billfish survival and minimize impacts on the target species catch.

Methods

The longline catch data were inspected 1) to determine the species composition of the catch to identify the set of species which, taken together, constitute the primary targets of the fishery, and 2) to identify possible trends in the reporting of billfish bycatch. The reported bycatch of billfish declined markedly in 1992 compared with earlier years. Consequently, the data were partitioned into two periods: 1986–91 and 1992–95. Data from the first period were used to characterize the spatial and temporal distributions of the catch. Data from the second period were used to test temporal stability of the results of analyses of the first period.

The billfish bycatch and the combined billfish (sailfish, spearfish, and blue and white marlin) bycatch as well as the target species catch for each longline set of each reported trip were summed into cells of 1°, 2°, and 5° latitude and longitude and month over the period 1986–91. The analysis was also repeated and only blue and white marlin bycatch was considered along with the target catch. Separate cumulative frequency distributions of the percentage of billfish or marlin bycatch in the combined billfish and target species catches by number by cell were constructed for each level of spatial resolution. These frequency distributions were used to estimate the percent reduction in billfish bycatch and target species catch that would have occurred if the effort in time–area cells with billfish or marlin bycatch rates above an arbitrary threshold had been completely eliminated during the 1986–91 fishery. The distribution of the minimum number of cells producing any specific reduction in billfish or marlin catches with the least impact on target species catch could then be determined from these data.

As an example, the distribution of cells that, if they had been eliminated from the 1986–91 U.S. fishery, would have reduced the billfish and marlin bycatches by 50%, were plotted for examination. Although the reporting rate declined after 1991, the temporal and spatial relative distributions of billfish in the total longline catch would be unaffected, so long as the change in the reporting rate was random. Consequently, the temporal stability of the reduction in billfish and marlin bycatch for the time–area cells identified with the 1986–91 data was evaluated by using data from 1992 to 1995. This was done by calculating the percent reduction in the total billfish and marlin bycatch that would have occurred each year if the time–area cells identified in the 1986–91 data had been closed. This analysis assumed that the displaced effort would not shift elsewhere.

Results

The catch by species in the data file from U.S. pelagic longline logbooks from 1986 through 1995 is presented in Table 1. Inspection of these data indicates that the predominant target species of this fishery included swordfish, yellowfin tuna, bigeye tuna, albacore, and dolphin fish. Together they constituted 90% of the nonbillfish harvest that was reported in these logbooks. For this analysis, billfish bycatch is the combined catch of sailfish, spearfish, and blue and white marlin, and marlin bycatch is the combined catch of blue and white marlin. Inspection of the data in Table 1 indicates a sharp drop in the numbers of billfish caught after 1991. This is possibly a consequence of a change in reporting trends following the U.S. billfish management plan's prohibition of the sale of billfish, or the restrictions on landing undersized swordfish imposed in mid-1991, rather than a consequence of a true reduction in the bycatches of billfish by the U.S. pelagic-longline fleet. Although no observer data are available before 1992, this conclusion is supported by data collected by observers on longline vessels that indicate billfish bycatch rates after 1992 were much higher than those reported in the logbooks (Cramer[1]). For this reason, the longline logbook data were grouped into two periods: 1986–91 and 1992–95. Data from 1986 through 1991 were used to characterize the distribution of billfish and target species catches, and data from 1992 through 1995 were used to test the spatial and temporal stability of the patterns observed in the 1986–91 data.

The percentage of billfish in the combined billfish bycatch and target species catch for each month–area cell in strata of 1°, 2°, and 5° was estimated, and the results were sorted to obtain cumulative frequency distributions of the billfish bycatch percentages for each spatial resolution. At the same time, the cumulative catches of billfish and target species were compiled for each observation in the cumulative frequency distributions of percentage of billfish in the catch in each time–area cell. The results of this procedure are presented in Figure 1 and Table 2. Note

[1] Cramer, J. 1996. Pelagic longline billfish bycatch. International Commission for the Conservation of Atlantic Tunas (ICCAT) working document SCRS/96/97.

Table 1

Catch in number (not including billfish discards) by species reported in the logbook data for U.S. pelagic longlines for 1986–95.

Species	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Swordfish	16,510	113,665	161,980	171,344	129,147	86,586	67,004	64,724	63,913	72,520	947,393
Bluefin tuna	58	484	422	717	599	540	1010	342	335	266	4773
Albacore	1181	2085	2984	3986	8220	9873	14,137	13,636	18,795	21,810	96,707
Bigeye tuna	3162	15,919	15,249	19,764	16,947	18,250	15,239	21,446	22,859	25,363	174,198
Yellowfin tuna	9241	59,665	67,569	83,844	68,711	70,433	94,510	68,360	73,337	85,135	680,805
Blackfin tuna	64	560	808	1450	1090	1525	3178	2797	3096	2363	16,931
Skipjack tuna	0	0	0	0	0	1384	2165	1374	232	279	5434
Bonito	0	0	0	0	0	0	0	238	1030	497	1765
Other tuna	0	0	0	0	0	0	1695	613	337	451	3096
Blue marlin	115	815	387	65	82	55	3	64	62	23	1671
Sailfish	4	55	147	53	66	22	5	34	56	87	529
Spearfish	4	52	47	2	15	2	8	30	19	14	193
White marlin	217	998	468	97	48	62	13	36	27	20	1986
Greater amberjack	0	0	0	0	0	0	112	836	1278	234	2460
Banded rudderfish	0	0	0	0	0	0	3	13	29	86	131
Dolphin fish	972	7861	10,768	29,899	31,899	32,576	25,351	26,142	29,617	72,321	267,406
King mackerel	1	11	35	119	11	67	118	4602	7176	1929	14,069
Wahoo	40	1346	2629	3157	3560	3736	6506	4393	3442	5477	34,286
Oilfish	0	0	0	0	0	0	0	37	5073	5102	10,212
Blue shark	944	1482	581	980	633	753	2050	1513	864	373	10,173
Mako shark	486	4055	4877	6946	4380	3475	414	338	371	187	25,529
Shortfin mako shark	0	0	0	0	0	0	3944	3738	3982	3747	15,411
Oceanic whitetip shark	0	0	0	0	0	0	319	226	166	205	916
Porbeagle shark	0	0	0	0	0	0	41	675	1591	509	2816
Bigeye thresher shark	0	0	0	0	0	0	200	304	626	472	1602
Other pelagic shark	0	0	0	0	0	0	0	0	0	8	8
Thresher shark	32	674	632	488	280	194	113	139	95	181	2828
Dusky shark	0	0	0	0	0	0	3365	7305	2826	2830	16,326
Bignose shark	0	0	0	0	0	0	70	254	124	123	571
Blacktip shark	0	0	0	0	0	0	3527	5965	6042	3954	19,488
Hammerhead shark	57	129	535	979	500	262	360	562	508	349	4241
Scalloped hammerhead shark	0	0	0	0	0	0	292	267	646	375	1580
Smooth hammerhead shark	0	0	0	0	0	0	627	452	484	231	1794
Night shark	0	0	0	0	0	0	478	455	379	421	1733
Silky shark	0	0	0	0	0	0	1685	1244	2134	2765	7828
Spinner shark	0	0	0	0	0	0	925	255	234	209	1623
Tiger shark	27	104	1051	183	98	108	165	173	477	202	2588
Other sharks	842	5740	4380	5424	9750	4620	3242	4242	1092	1376	40,708
White shark	20	137	1723	1222	537	95	104	163	16	2	4019
Sandbar shark	0	0	0	0	0	0	0	0	2020	14,192	16,212
Other	0	0	0	0	0	0	0	0	90	2515	2605

that the initial slope of the relation between the billfish percent reduction and target species percent reduction is much lower than 1.0 for each of the spatial resolutions examined. This finding suggests that the temporal and spatial distributions of billfish bycatch and target species are somewhat different and that it should be possible to selectively reduce the longline billfish bycatch in relation to target species catch. The data from Table 2 indicate that a 10% reduction in the 1986–91 billfish bycatch could have

Table 2

Estimated reduction in billfish bycatch and target species catch by elimination of time–area cells where the billfish percentage of catch is greater than or equal to the specified threshold value based on 1986–1991 catch rates in the U.S. pelagic-longline fishery. These estimates assume that the displaced effort will not be redirected elsewhere.

	1° cells		2° cells		5°cells	
Billfish reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)
5	18.46	0.34	14.23	0.49	9.64	0.94
10	14.32	1.01	9.99	1.51	8.77	2.33
15	12.06	1.90	9.44	2.73	7.94	3.88
20	10.07	2.97	8.52	4.08	7.58	5.52
25	8.81	4.25	7.17	5.62	7.34	7.21
30	7.52	5.74	5.86	7.54	6.10	9.19
35	6.78	7.45	5.47	9.70	5.70	11.38
40	6.16	9.37	4.87	12.13	5.52	13.68
45	5.49	11.49	4.61	14.77	4.86	16.29
50	4.95	13.87	4.32	17.57	4.36	19.17
55	4.37	16.59	4.10	20.53	4.21	22.28
60	4.03	19.59	3.79	23.72	3.95	25.51
65	3.61	22.85	3.51	27.16	3.57	29.11
70	3.30	26.53	3.21	30.92	3.11	33.13
75	2.94	30.62	2.95	35.01	2.76	37.67
80	2.56	35.30	2.48	39.73	2.46	42.92
85	2.17	40.73	2.19	45.21	2.07	48.85
90	1.74	47.38	1.70	52.09	1.73	55.91
95	1.20	56.08	1.15	61.54	1.26	65.08

been attained with only a 1 to 2.3% reduction in the catch of target species, depending on the spatial resolution employed. This reduction would have been achieved by eliminating the effort in months and areas where the reported billfish bycatch exceeded the threshold percentage of billfish in the combined catch in Table 2. Similarly, a 50% reduction in the 1986–91 billfish bycatch would have been achieved by eliminating the effort in cells where the reported billfish bycatch exceeded the table values with corresponding reductions of 13.9 to 19.2% in the harvest of target species. A 95% reduction in the 1986–91 billfish bycatch would have been achieved by eliminating all effort in cells with reported catches of more than 1.2, 1.15, or 1.26% billfish for 1°, 2°, or 5° cells, and there would have been a concomitant reduction in target species catch of 56.1, 61.5, or 65.1%, respectively.

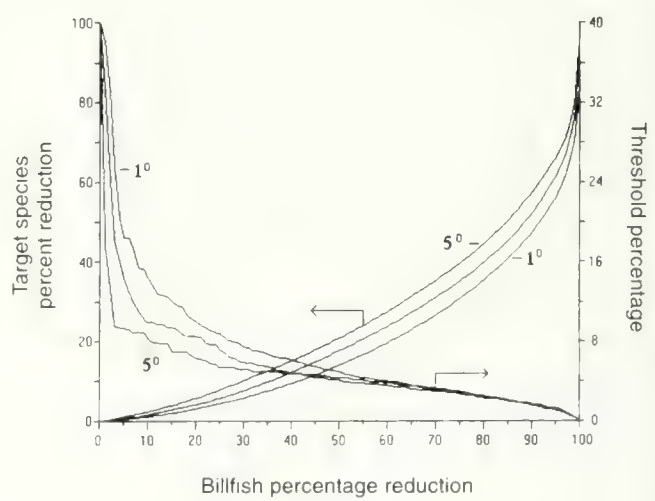


Figure 1

Percent reduction in target species and marlin bycatch associated with the removal of effort in time–area cells above the indicated threshold percentage of all billfish in the catch for cell sizes of 1°, 2°, and 5° of latitude and longitude.

The same type of analysis was conducted with only blue and white marlin as the billfish species of concern. The results are presented in Figure 2 and Table 3. As with billfish combined, the initial slope of the relation between the percent catch of marlin bycatch and of target species is much less than 1.0. This result also indicates that the combined marlin bycatch can be reduced by the elimination of select time–area strata and that the catch of target species would not be proportionately affected. The data from Table 3 indicate that a 10%

Table 3

Estimated reduction in blue and white marlin bycatch and target species catch by elimination of time–area cells where the marlin percentage of catch is greater than or equal to the specified threshold value based on 1986–91 catch rates in the U.S. pelagic-longline fishery. These estimates assume that the displaced effort will not be redirected elsewhere.

	1° cells		2° cells		5° cells	
Marlin reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)	Threshold (%)	Target reduction (%)
5	18.15	0.38	11.54	0.53	7.32	1.11
10	10.16	1.14	7.06	1.71	6.22	2.79
15	7.71	2.34	5.19	3.50	5.49	4.76
20	6.17	3.79	4.79	5.37	5.21	6.33
25	5.77	5.10	4.24	7.44	4.83	8.62
30	4.97	6.80	4.02	8.99	4.65	10.81
35	4.54	8.57	3.87	11.59	4.16	13.63
40	4.15	10.95	3.64	14.14	4.02	15.70
45	3.78	13.60	3.44	16.55	3.86	17.72
50	3.46	16.37	3.23	19.55	3.58	20.74
55	3.24	19.50	3.12	22.44	3.12	23.66
60	3.00	22.03	2.87	25.95	2.84	27.44
65	2.76	25.04	2.67	29.47	2.68	30.54
70	2.39	28.50	2.39	32.87	2.47	34.89
75	2.14	32.94	2.10	36.53	2.20	38.76
80	1.86	37.90	1.85	41.40	2.01	44.08
85	1.56	43.97	1.67	46.43	1.78	49.78
90	1.21	50.49	1.23	53.72	1.49	56.75
95	0.73	59.39	0.84	63.06	1.07	66.45

reduction in the 1986–91 marlin bycatch could have been attained with only a 1.1 to 2.8% reduction in the catch of target species, depending on the spatial resolution employed. This would result by eliminating the effort in months and areas where the reported billfish bycatch exceeded the threshold percentage of billfish in the combined catch indicated in Table 3. Similarly, a 50% reduction in the 1986–91 marlin bycatch would have been obtained by eliminating the effort in cells where the reported billfish bycatch exceeded the table values with corresponding reductions of 16.4 to 20.7% in the harvest of target species. A 95% reduction in the 1986–91 marlin bycatch would have been achieved by eliminating all effort in cells that reported catches of more than 0.73, 0.84, or 1.07% marlin for 1°, 2°, or 5° cells, and there would have a concomitant reduction in target species catch of 59.4, 63.1, or 66.5% respectively.

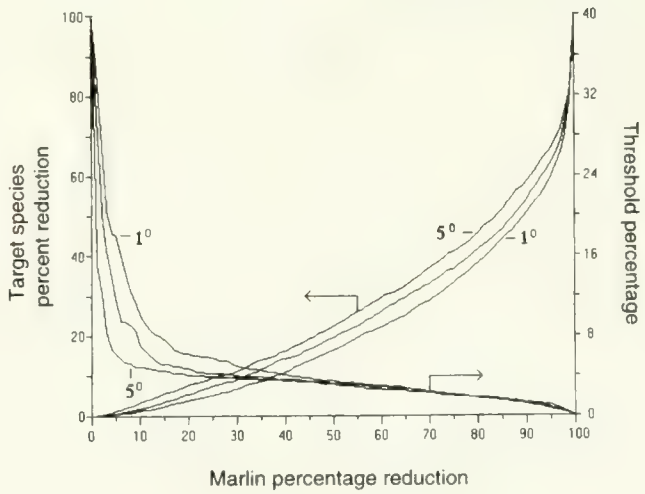


Figure 2

Percent reduction in target species and blue and white marlin bycatch associated with the removal of effort in time–area cells above the indicated threshold percentage of marlin in the catch for cell sizes of 1°, 2°, and 5° of latitude and longitude.

Obviously, the temporal and spatial distribution of the cells that would be eliminated with the current method for any particular threshold selected is of considerable interest. Figure 3 presents the distribution of cells by area and month that correspond to a threshold selection that would have eliminated 50% of the billfish bycatch from the 1986–91 U.S. pelagic-longline fishery as reported in the log books. Areas where fishing effort was expended within 5° cells are stippled or diagonally

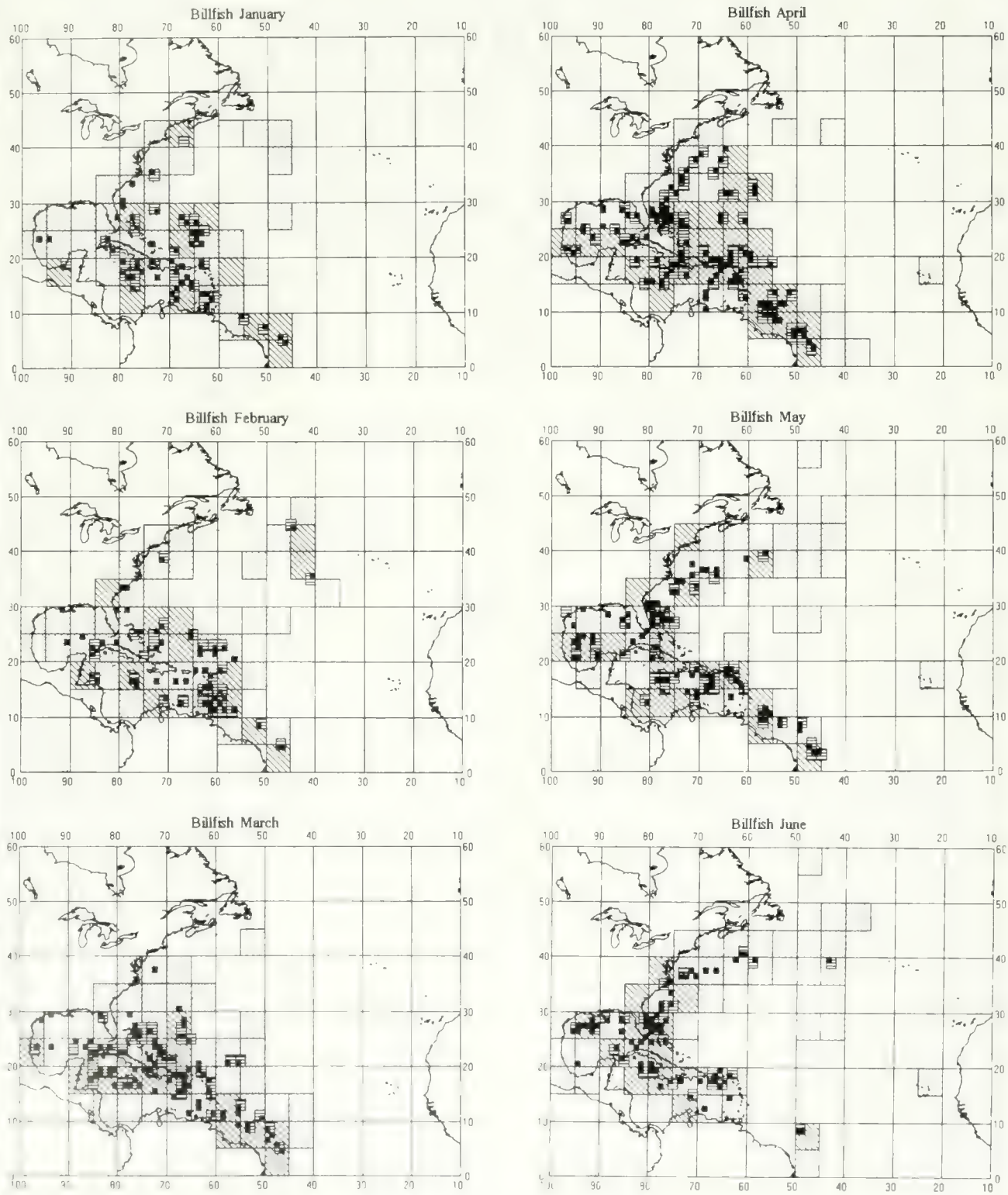
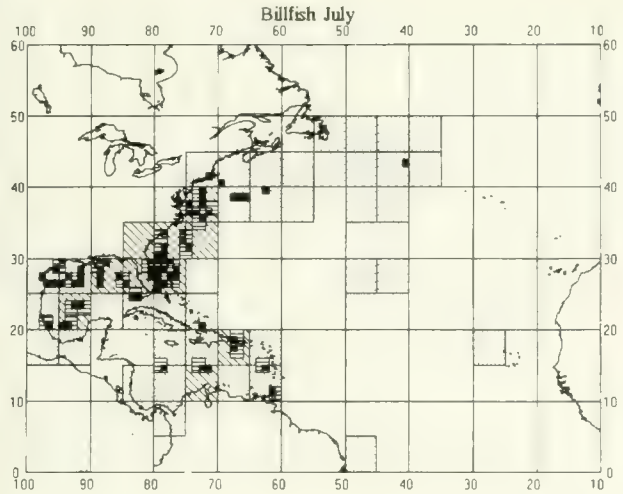
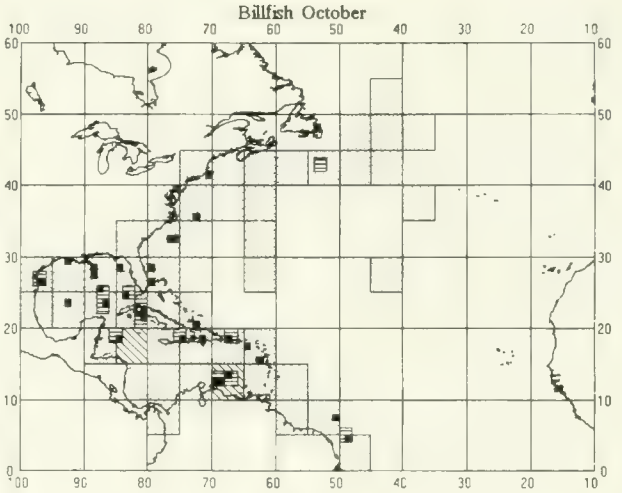
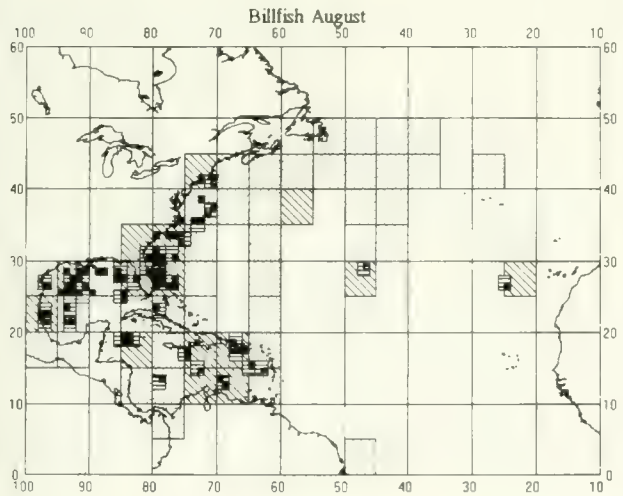


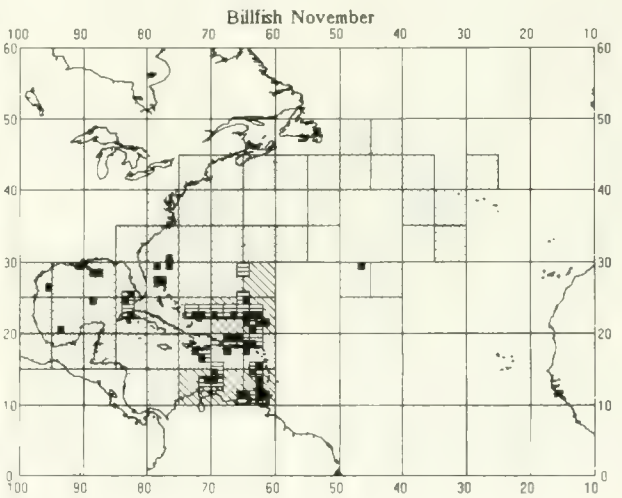
Figure 3

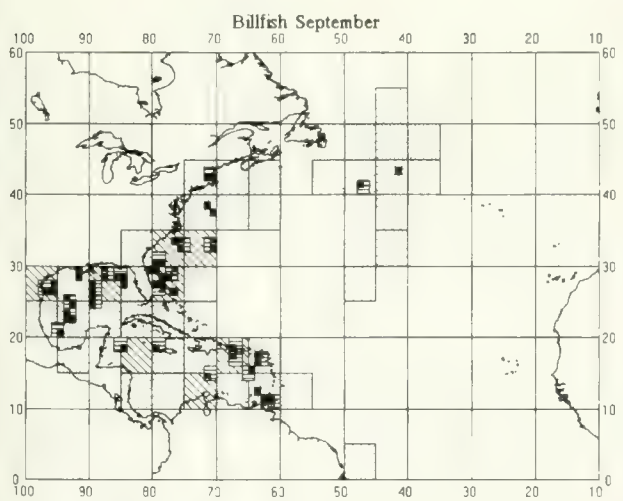
Distribution of 1986–91 U.S. pelagic-longline fishing effort by month and area fished (stippled or diagonally shaded cells of 5° cell or smaller. Month–area cells where billfish bycatch percentages were greater than the 50% threshold levels for 1° (filled), 2 (horizontal shading) and 5° (diagonal shading) cells. Elimination of the effort in these cells would have reduced the combined billfish bycatch by 50% and reduced the target species catch by 13.9, 17.6, and 19.2% respectively.











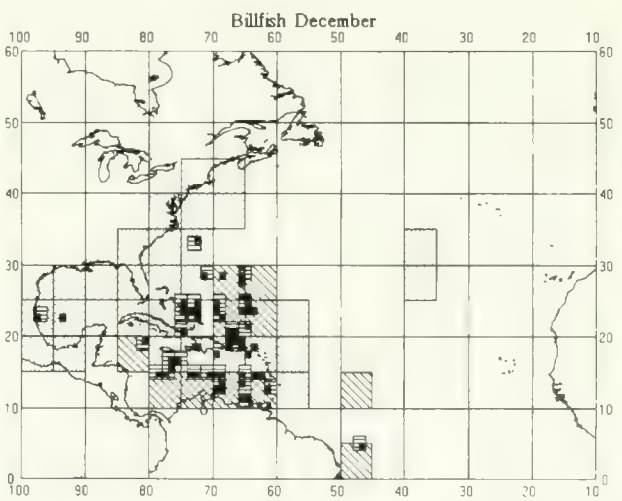


Figure 3 (continued)

shaded. The diagonally shaded 5° cells indicate where the billfish proportion of the catch within the 5° area exceeded the 4.36% threshold required to obtain a 50% reduction in the 1986–91 billfish bycatch indicated in Table 2. The horizontally shaded 2° cells indicate those cells where the billfish proportion exceeded the threshold for the 2° spatial resolution, and the filled 1° cells indicate those cells where the billfish proportion exceeded the 1° threshold. Inspection of these plots indicates a temporal pattern in the distribution of fishing effort—from southern waters in the winter to northern and eastern waters during the summer and fall. Also the minimum number of cells that would have to have been eliminated from the 1986–91 fishery to reduce the billfish bycatch by 50% occur during the months of September through November. There is also a tendency for the affected cells to move north from the southernmost regions fished in November and December to the entire U.S. coastline by July and August.

Similar plots are presented for marlins in Figure 4, with the respective threshold percentages of marlin in the catch. As for billfishes combined, the number of cells above the threshold percentages is at a minimum in October but increases thereafter to a peak in April. The affected cells move north during the spring and summer from primarily southern latitudes in the winter. However, some cells in the Caribbean exceed the 50% thresholds of Table 3 in almost every month.

To test the temporal and spatial stability of the areas identified in Figures 3 and 4, I calculated the percent reductions in billfish and marlin bycatch and target species that would have occurred if those areas had been closed in each year from 1992 through 1995 for each level of spatial resolution considered (Tables 4 and 5). These estimates assumed that the time–area strata identified for closure would not be redirected elsewhere but did include strata fished in 1992–1995 that were not present in the 1986–91 base period. For billfish combined, billfish would have been selectively protected by closing the time–area cells identified from the 1986–91 data evaluation each year from 1992 through 1995 with all levels of spatial resolution examined. The agreement between predicted and 1992–95 observed values increased with increasing grid size (Table 4). Mean billfish reductions increased from 28.6% to 41.6% from 1° to 5° cells compared with the predicted levels of 50%. The mean reductions for targeted species were slightly less than the predicted values. The observed mean values were 12.8, 11.9, and 16.7%, compared with the predicted values of 13.9, 17.6, and 19.2% for the 1°, 2° and 5° cells, respectively. In general, the larger 5° grid produced results that were closest to the values predicted from the 1986–91 data set and showed the least year-to-year variability in the percent reduction of billfish bycatches.

For the analyses considering marlin species only, marlins would also have been selectively protected by closing the time–area cells identified from the 1986–91 data evaluation each year from 1992 through 1995 with all levels of spatial resolution examined. The agreement between predicted and 1992–95 observed values also increased with increasing grid size (Table 5) but were closer to the predicted values than for the evaluation of billfish combined. Mean marlin reductions increased from 35.7% to

Table 4

Evaluation of the temporal stability of the estimated percentage changes in billfish bycatches and target species catches using the time–area closures identified in the analyses of the 1986–91 longline data. The threshold levels were selected to reduce combined billfish bycatch by 50%, and the time–area cells that were excluded are those indicated in Figure 3. The estimated percentage reductions are based on the proportion of the annual total catch within the cells identified for closure and include areas fished in 1992–95 that had not been fished during the 1986–91 base period. The columns labeled "cells" are the percentages of the time–area strata fished during the year that would have been eliminated by closing the indicated cells.

	Predicted percentage reduction with billfish threshold model								
	1° cells			2° cells			5° cells		
Year	Billfish	Target	Cell	Billfish	Target	Cell	Billfish	Target	Cell
1992	24.5	11.7	15.7	25.8	10.7	14.1	42.2	15.7	20.3
1993	37.0	15.5	16.1	33.7	13.2	13.2	39.1	17.9	19.3
1994	32.1	13.6	19.1	35.5	12.7	14.7	44.5	17.8	20.7
1995	20.8	10.2	13.7	23.2	10.9	14.5	40.7	15.2	19.9
Mean	28.6	12.8	16.2	29.6	11.9	14.1	41.6	16.7	20.1

48.6% from 1° to 5° cells compared with the predicted levels of 50%. The mean reductions for targeted species were slightly greater than the predicted values. The observed mean values were 18.6, 20.1, and 22.8%, compared with the predicted values of 16.4, 19.6, and 20.7% for the 1°, 2° and 5° cells, respectively. As with billfish combined, the larger 5° grid produced results that were closest to the values predicted from the 1986–91 data set and showed the least year-to-year variability in the percent reduction of marlin catches. Overall, the result for marlin at the 5° resolution was in remarkable agreement with the values predicted from the evaluation of the 1986–91 data.

Discussion

This study was intended to consider pelagic longlines only. However, bottom-longline and pelagic-longline sets could not always be clearly distinguished in the database used for the analysis. Consequently, some of the effort and catch included in the analyses were likely from bottom-longline sets. Some additional refinement of the analyses might have been possible with additional attention to eliminating bottom-longline data. However, the total of the bottom-longline sets is thought to be only about 10% of the longline sets in the database (Cramer[2]), and all identified bottom-longline sets were eliminated from the analysis. Consequently, it is not likely that a complete elimination of the bottom-longline sets would have had an important effect on the basic pattern seen in the results of this study.

The International Commission for the Conservation of Atlantic Tunas (ICCAT) CPUE data files (task ii) indicate that billfish often accounted for 15% or more of the Japanese longline catch in the Gulf of Mexico and Caribbean before about 1977. However, the total harvest of billfish by the pelagic-longline fishery documented in the 1986–95 U.S. logbooks was never large in comparison with other species in their reported catch, and most were discarded even before the prohibition on harvest was promulgated by the U.S. Atlantic Billfish Plan. According to logbook records only 16.26% of the billfish caught during the period 1986–89 were retained. This figure dropped to 4.82% for the period 1992–95. Observer data for pelagic-longline trips indicate that the actual bycatch rates for billfish in this fishery are much higher than is currently being reported in logbooks (Cramer[1]). This phenomenon perhaps exists because billfish are not economically important components of the harvest, a phenomenon that was intensified by the U.S. Atlantic Billfish Plan which prohibited commercial harvest of billfishes after 1988. If so, it is likely that billfish were under-reported in the logbook data for the 1986–91 period used in the present analysis. The magnitude of the reporting rate is unknown for the 1986–91 period. However, unreported rates would not pose a problem for the analysis presented here if they were randomly distributed in time and space. This question could possibly be addressed in future analyses by using observer data from U.S. domestic pe-

[2] Cramer, J. 1996. Sustainable Fisheries Division, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

Table 5

Evaluation of the temporal stability of the estimated percentage changes in marlin and target species catches using the time–area closures identified in the analyses of the 1986–91 longline data. The threshold levels were selected to reduce marlin catch by 50%, and the time–area cells that were excluded are those indicated in Figure 4. The estimated percentage reductions are based on the proportion of the annual total catch within the cells identified for closure and include areas fished in 1992–95 that had not been fished during the 1986–91 base period. The columns labeled "cells" are the percentages of the time–area strata fished during the year which would have been eliminated by closing the indicated cells.

	Predicted percentage reduction with marlin threshold model								
	1° cells			2° cells			5° cells		
Year	Marlin	Target	Cell	Marlin	Target	Cell	Marlin	Target	Cell
92	24.7	15.0	17.8	41.0	18.2	19.7	48.9	20.4	23.3
93	38.3	19.8	18.6	43.8	20.8	17.8	45.3	22.7	19.8
94	44.9	21.5	20.5	47.0	20.4	17.3	47.6	23.1	23.2
95	35.0	18.2	16.2	45.8	21.1	18.2	52.5	24.9	22.7
Mean	35.7	18.6	18.3	44.4	20.1	18.3	48.6	22.8	22.2

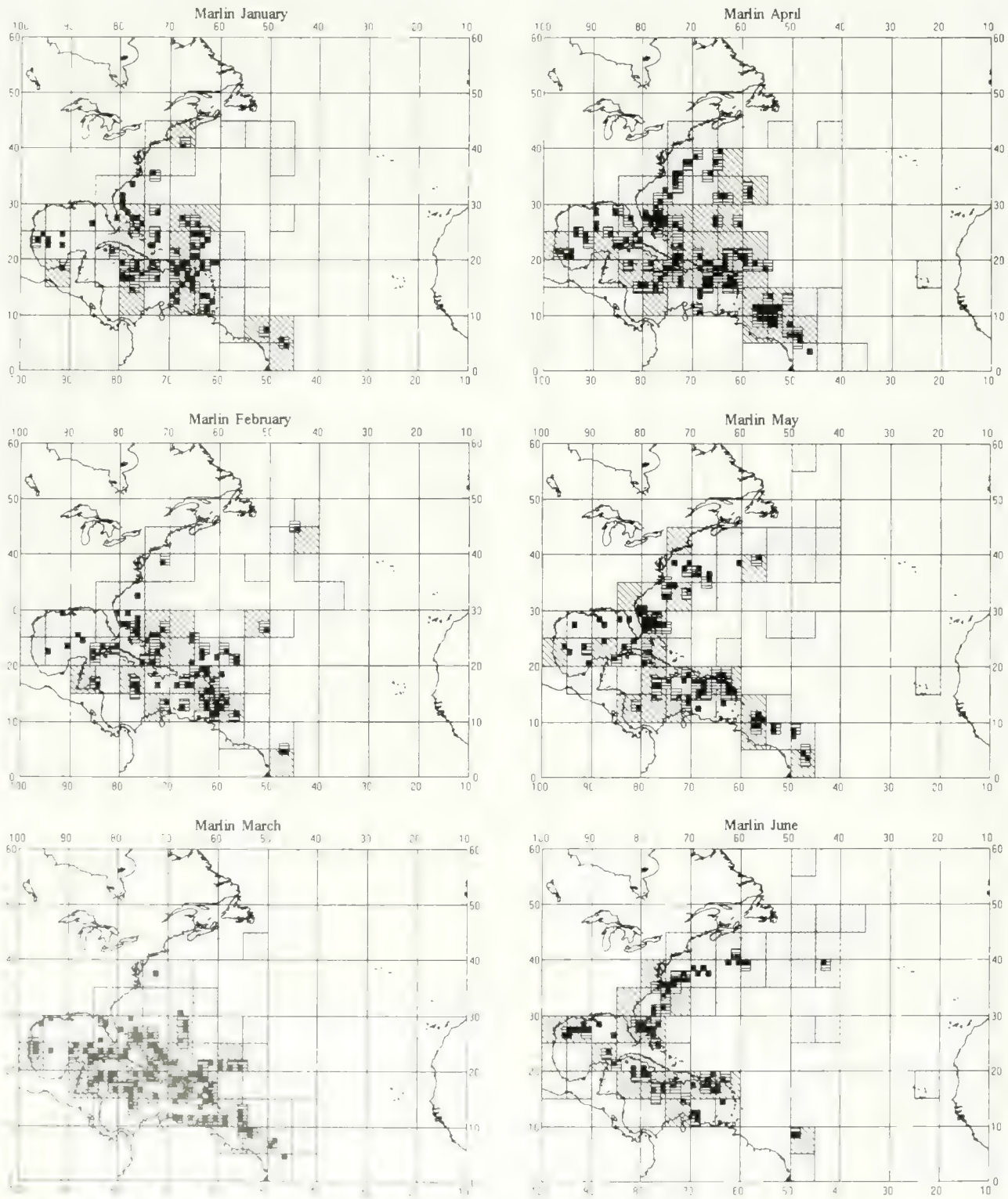


Figure 4

Distribution of 1986–91 U.S. pelagic-longline fishing effort by month and area fished (stippled or diagonally shaded cells of 5° cell or smaller. Month–area cells where marlin bycatch percentages were greater than the 50% threshold levels for 1° (filled), 2° (horizontal shading), and 5° (diagonal shading) cells. Elimination of the effort in these cells would have reduced the marlin bycatch by 50% and reduced the target species catch by 16.4, 19.6 and 20.7%, respectively.

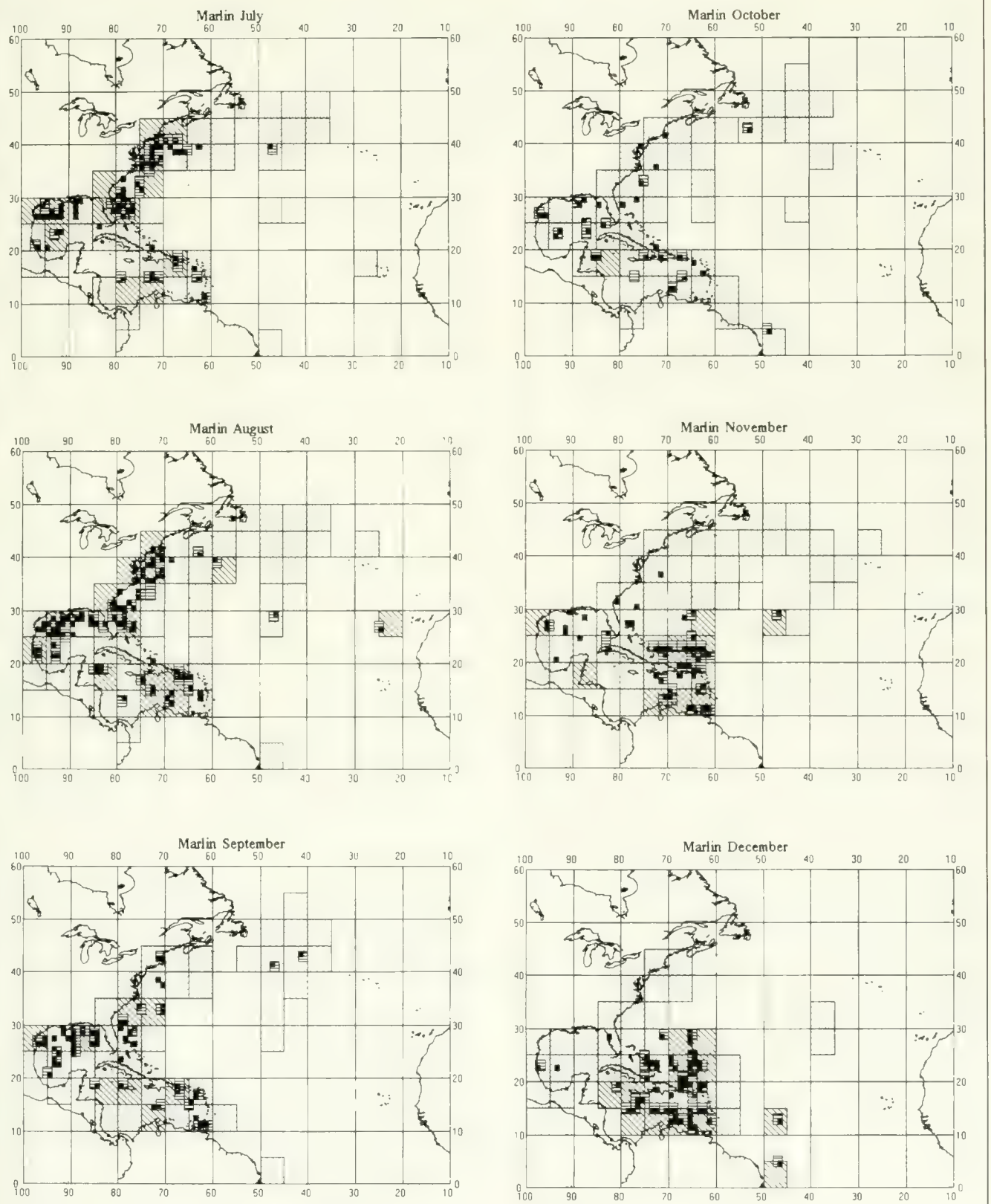


Figure 4 (continued)

lagic-longline vessels, although the amount of available data for the period is limited.

Although the study results demonstrate that time–area restrictions on the U.S. pelagic-longline fishery could substantially reduce the bycatch of billfish by this fishery, it is only a first step. As Murawski (1992) pointed out, any bycatch reduction plans involving time–area manipulation of the fishery should be economically viable and the proposed program must be effectively implemented and enforced. These issues were beyond the scope of the present study. An evaluation of the utility of time–area restrictions for reducing the mortality of billfish in the longline fishery must also consider aspects of the dynamics of the fishery itself. Among other considerations, the present analysis assumes that the effort eliminated by a time–area closure would not be redirected to some other time or area. The catch associated with a stratum removed by the selection of a particular threshold of percent billfish in the catch was simply removed from the total catch of both the billfish bycatch and target species. With no restriction on total effort, it seems more likely that the affected effort would be redirected into some other area, and the total billfish bycatch, although reduced, would not be reduced by the magnitude indicated in Tables 2 and 3 (and of course, neither would the target species). Analyses that consider the possible redirection of effort would need to include socioeconomic considerations about the nature and dynamics of the pelagic-longline fishery. Also catch limitations arising from the U.S. allocation of total allowable catches of the various target species by ICCAT could be integrated into the analysis. The focus of such an analysis would be to minimize the billfish bycatch by selecting fishing areas that would maximize the catch rates of target species in areas of minimal billfish bycatch. This could both promote efficient use of the target resources and the reduction of billfish bycatch. Similarly, other management objectives could be integrated into the time–area question.

Although, such extensions of the methods presented here should prove fruitful for the selection of actual management restrictions, the results of this study clearly indicate that the relative time and areal distributions of billfish and target species in the pelagic-longline catch are different. This difference can be exploited to reduce the billfish bycatch in this fishery with less than a proportional effect on the catch of targeted species. A next step toward identifying realistic management measures could be the characterization of reasonable, contiguous geographic areas where pelagic-longline closures would be both practical and of the greatest benefit to increased billfish survival. However, because U.S. vessels are a small part of the total Atlantic pelagic-longline fishery, greatest gains from this approach would necessarily involve participation of the pelagic-longline fleets from other countries.

Acknowledgments

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Age validation and analysis of ageing error from marked and recaptured sablefish, *Anoplopoma fimbria*

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Abstract.—Sablefish, *Anoplopoma fimbria*, are especially difficult to age. Ages are typically determined by counting growth zones that are assumed to be annuli on the burnt cross section of an otolith. We evaluated the accuracy of ageing methods by comparing the ages obtained from two experienced age readers with those ages that were known. A mark-recapture experiment on sablefish provided a relatively large sample (n=49) of 2–9 year old sablefish. This sample of known-age fish provided a unique opportunity to evaluate the accuracy of ageing methods for young sablefish. Our study generally confirmed the criteria used to age young sablefish. According to the assignment of ages from two experienced age readers, about two-thirds of the fish were misaged. Of these, most fish (81% and 71% for the two readers) were misaged by only one year. After reexamination of the otoliths, most of the discrepancies between reader age and known age could be resolved. Ageing-error matrices that define the probability of assigning an age to a fish of a given true age were estimated from among-reader variability and from comparison of known ages to reader ages. Estimates of ageing errors, based on comparison of known ages to reader ages, were considerably higher than estimates obtained from among-reader variability. We recommend that ageing-error corrections applied in stock assessment models be based on the ageing-error matrix derived from known and reader ages.

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Errors in fish ageing may result in biases in stock assessments and possible mismanagement of fisheries. Estimates of natural mortality, age composition, growth parameters, and maturity schedules of a fish population all depend on accurate ageing for their reliability. Thus, valid ageing is a key to understanding the biology and dynamics of fish populations.

Ageing error in stock assessment models can lead to errors in modeling results (Kimura, 1990). Ageing errors tend to smooth differences in year-class strengths and may confound attempts to estimate stock recruitment relationships and to relate year-class strength to environmental factors (Fournier and Archibald, 1982; Richards et al., 1992). Estimation of ageing errors enables such errors to be accounted for by allowing observed ages to be converted back to correct ages (Richards et al., 1992). If misspecified or unaccounted for, ageing error can lead to erroneous yield projections and overfishing (Lai and Gunderson, 1987; Tyler et al., 1989).

Sablefish, aged as old as 63 years in Alaska (Sigler et al., 1997), is an especially difficult species to age (Kimura and Lyons, 1991). Beamish and Chilton (1982) first suggested that sablefish was a much longer-lived species than previously thought and proposed an ageing method using broken and burnt otoliths that would result in more accurate ages. Preliminary data from their tagging studies, otoliths marked with oxytetracycline (OTC), and a small sample (n=6) of known-age fish appeared to validate this new method. Results from subsequent studies with recaptured OTC-marked fish (Beamish et al., 1983; McFarlane and Beamish, 1995), a small sample of pen-reared fish (Lai, 1985), and radiometric ageing (Kastelle et al., 1994) have further substantiated the reliability of this method. This break-and-burn method is now widely accepted by sablefish age readers. Sablefish is still a very

difficult species to age, and age determination is highly subject to an age reader's interpretation.

For this paper, sablefish tagged and released as young juveniles (Rutecki and Varosi, 1997a) provided a relatively large sample (n=49) of known-age fish, 2–9 years old when recaptured. This sample provided a unique opportunity to evaluate the accuracy of production ageing methods for young sablefish. "Production ageing" is the routine ageing of large samples of fish, usually to obtain age and growth information or age composition. We conducted a statistical analysis of ageing errors and compared ageing errors based on among-reader agreement with ageing errors based on reader and known-age agreement.

Materials and methods

Known-age fish

From 1985 to 1991 about 23,000 age 0–2 sablefish were tagged with individually numbered Floy anchor tags (Rutecki and Varosi, 1997a, 1997b). By 31 December 1993, 1160 of these fish had been recaptured, mostly from commercial fishing operations; otoliths were taken from 49. In Rutecki and Varosi's studies, cohorts of young (aged 0–2) sablefish were periodically sampled in interior bays of southeastern Alaska from spring through early fall. Depending on the time of year, usually only one or two age classes were present at the sampling locations, and these age classes could be distinguished easily from one another on the basis of nonoverlapping length frequencies (see Figs. 5 and 7 in Rutecki and Varosi [1997b]). Rutecki and Varosi (1997b) confirmed assignment of ages by ageing otoliths from a subsample of the fish measured for length. Of the 49 known-age sablefish, one was tagged at age 0, 41 at age 1, and seven at age 2. Known age of a fish was calculated by subtracting the year of release from the year of recapture and then adding the age at release. For example, the known age of a fish tagged in 1986 at age 1 and recaptured in 1992 would be 7 years.

Ageing methods

Extracted otoliths were stored in a 50% ethyl alcohol solution. A sample of otoliths from 140 fish, including the 49 known-age fish, were aged by two experienced readers in the Age and Growth Laboratory at the Alaska Fisheries Science Center (AFSC) in Seattle, Washington. Using normal production ageing procedures, the readers were told the fork length of each fish and the month and day of sampling. The year of sampling was withheld. Age readers were aware that known-age otoliths were in the sample but did not know what percentage of the sample were known-age specimens nor the age range of the known-age fish.

The primary age reader (hereafter referred to as "primary reader") prepared all the otoliths and was first to examine the sample. The ageing methods generally followed Beamish and Chilton (1982). The ageing routine began with placing each otolith in a water-filled petri dish with a black background and examining it through a light microscope with fiber-optic light. This gave the primary reader a general idea of an age range to expect before the otolith was broken and burned. Next, the otolith was broken dorsoventrally along the focus, and the broken surface was passed over a flame. The burnt half was then mounted into clay for support, and the burnt surface was coated with cedar oil for clarification. The burnt surface consisting of light and dark zones was then examined by using a light microscope and fiber-optic light. The light areas are known as opaque zones and the dark areas as translucent zones. Notes kept by the reader included the reasons for ageing decisions when uncertainties occurred. Typically in production ageing, an age reader may opt not to assign an age to an otolith if the otolith pattern or condition is considered so poor that the reader's confidence at reproducing roughly the same age again is questionable; this policy was followed in our study.

In production ageing at the AFSC, after the primary reader completes the age determinations, another reader (hereafter referred to as the "tester") typically rereads a 20% random sample of the otoliths without knowledge of the primary reader's ages. This is done mainly to control quality (Kimura and Lyons, 1991). Because the known-age specimens were not known to the readers, the randomly chosen 20% sample included only 10 of the known-age otoliths. To compare agreement on all known-age otoliths, a second subsample was drawn, which included all the remaining known-age otoliths interspersed with some unknown-age otoliths. The tester did not know the percent composition of known- to unknown-age otoliths in either subsample.

In addition to the ageing methods of Beamish and Chilton (1982), in production ageing at the AFSC, readers use the marginal increment component for ageing, i.e. they decide whether the most recent year's annulus was formed along the margin of an otolith. Many experienced sablefish age readers have concluded that the annulus usually forms in spring, but some annuli may form in summer. However, an age reader must decide whether an annulus was deposited before the date of otolith collection by considering the date of the otolith collection and the amount

of otolith growth between the last annulus and the otolith margin. If the otolith was collected in the spring or summer and there is a relatively large area of growth along the otolith margin, an age reader would probably decide that the annulus had not yet been deposited and would therefore add 1 to the number of annuli observed on the otolith. However, if a relatively small area of growth is seen, then the reader would probably assume that the annulus had been deposited and assign an age equal to the number of annuli observed. By fall and winter, the current year's annulus is expected to have been deposited, and the fish age would, therefore, equal the number of annuli observed on the otolith.

Analysis of ageing errors

Present stock assessment of sablefish and many other groundfish species in Alaska is based on an age-structured model that attempts to estimate the true age composition of the population (Sigler et al.[1]). Ageing errors in catch-age models can be accounted for by supplying an ageing-error matrix (Fournier and Archibald, 1982; Methot, 1990; Richards et al., 1992). This matrix defines the probability of assigning a particular age to a fish with a given true age. The results of multiple age determinations from independent age readings can be used to estimate the ageing-error matrix (Richards et al., 1992). In practice, a normal distribution of observed age for each true age is assumed and because ageing error tends to increase with age, an increase in the standard deviation with increasing age is used (Lai and Gunderson, 1987; Methot, 1990). Use of multiple readings to assess ageing errors cannot detect a systematic difference (i.e. bias) between observed and true ages (Richards et al., 1992).

We constructed two ageing-error matrices to illustrate the possible difference in perceived ageing error based on agreement between primary reader and tester and between reader and known age. The first matrix was based on primary-reader and tester ages and the second was based on reader (both primary reader and tester) and known ages.

Richards et al. (1992) presented a statistical model for estimating ageing error. We used the "normal model" of Richards et al. (1992). For a given true age b, the standard deviation $\sigma(b)$ of the observed age is defined by three parameters σ_1, σ_A, and α such that

$$\sigma(b) = \begin{cases} \sigma_1 + (\sigma_A - \sigma_1)\dfrac{1 - e^{-\alpha(b-1)}}{1 - e^{-\alpha(A-1)}}; & \alpha \neq 0 \\ \sigma_1 + (\sigma_A - \sigma_1)\dfrac{b-1}{A-1}; & \alpha = 0 \end{cases} \quad (1)$$

The σ_1 and σ_A are standard deviations for the minimum and maximum ages, respectively. The parameter α determines the nonlinearity of the function, where $\sigma(b)$ becomes linear in b as α tends to 0. Given the parameter vector $\mathbf{\Phi} = (\sigma_1, \sigma_A, \alpha)$ and observed age classes a, the age-error matrix $q(a \mid b, \mathbf{\Phi})$ is defined by

$$q(a|b,\mathbf{\Phi}) = \frac{x_{ab}(\mathbf{\Phi})}{\sum_{a=1}^{A} x_{ab}(\mathbf{\Phi})}, \quad (2)$$

where $x_{ab}(\mathbf{\Phi})$ is the discrete normal density function such that

$$x_{ab}(\mathbf{\Phi}) = \frac{e^{-\frac{1}{2}\left[\frac{a-b}{\sigma(b)}\right]^2}}{\sqrt{2\pi\sigma(b)}}. \quad (3)$$

In Richards et al. (1992), the assumed "true age" for a fish aged by multiple readers is the modal age among multiple readers. We used the mean age rounded to the nearest integer because the mode is not defined for two readings when the ages differ. For the reader and known-age data, the true age is the known age. A value for the maximum age A is required. For the reader and known-age data set, we set A equal to the maximum known age. For the primary reader and tester data set, we set A equal to the maximum assigned age.

The model of Richards et al. (1992) does not include estimation of bias. The use of known ages allows bias to be estimated and incorporated in the ageing-error matrix. By including three additional parameters, Ericksen (1997) generalized the methods of Richards et al. (1992) to include estimation of bias for tag recapture and known-age data. As with Equation 1, for a given true age b, the bias $\beta(b)$ of the observed age is defined by three parameters, β_1, β_A, and λ, such that $\mathbf{\Phi} = (\sigma_1, \sigma_A, \alpha, \beta_1, \beta_A, \lambda)$ and

$$\beta(b) = \begin{cases} \beta_1 + (\beta_A - \beta_1)\dfrac{1 - e^{-\lambda(b-1)}}{1 - e^{-\lambda(A-1)}}; & \lambda \neq 0 \\ \beta_1 + (\beta_A - \beta_1)\dfrac{b-1}{A-1}; & \lambda = 0 \end{cases} \quad (4)$$

Equation 3 is modified to obtain

[1] Sigler, M. F., J. T. Fujioka, and S. A. Lowe. 1997. Sablefish. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fish. Manage. Council, 605 W 4th Ave., Suite 306, Anchorage, AK 99501.

$$x_{ab}(\mathbf{\Phi}) = \frac{e^{-\frac{1}{2}\left[\frac{a-b+\beta_1 b+\gamma}{\sigma_1 b}\right]^2}}{\sqrt{2\pi\sigma(b)}}. \qquad (5)$$

To estimate the classification matrix defined by Equation 2, maximum likelihood was used to estimate the parameters of the model. The likelihood (L) of the observed ages **A** given the true ages **B** is

$$L(\mathbf{A}|\mathbf{B}) = \prod_{i=1}^{I}\prod_{j=1}^{J} q(a_{ij}|b_i, \mathbf{\Phi}), \qquad (6)$$

where a_{ij} = the age assigned to fish i by reader j; and
b_i = the true age of fish i.

In practice, the inference function $-2 \log L(\mathbf{A}|\mathbf{B})$ is minimized to obtain parameter estimates. Given the number of parameters N, the Akaike information criteria (AIC) (Akaike, 1974; Richards et al., 1992),

$$AIC = -2\log L(\mathbf{A}|\mathbf{B}) + 2N, \qquad (7)$$

was used in the model identification process. A model with a low AIC value in relation to other models is considered the best-fit model with the fewest parameters.

Six alternative representations (cases) of ageing error were considered in the analysis. The different cases represented the two different data sets, full models, and models reduced by parameter constraints (Table 1). Although not within the scope of our study, we recognize other alternative model specifications may be appropriate for these data sets. For example, a classification matrix with skewed distributions of the probability of assigning an age to a fish of a given true age may be appropriate.

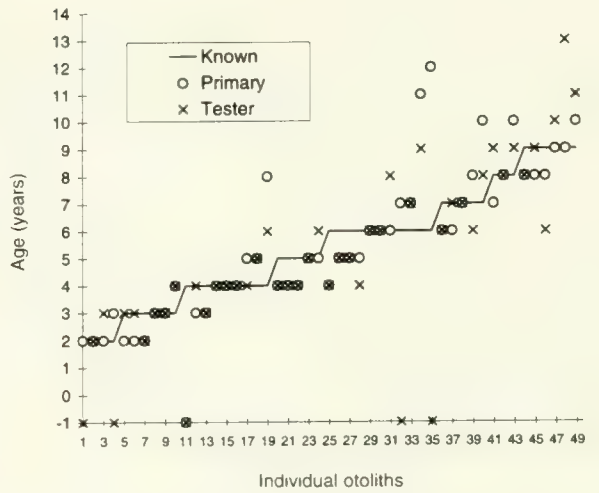

Figure 1

Comparison of known age with ages obtained by two age readers for 49 sablefish. A value of –1 for a age denotes the reader chose not to age the given sample. The x-axis has been sorted by known age from youngest to oldest.

Table 1

Alternative cases for analysis of ageing error based on primary reader and tester data (data set 1) and reader and known-age data (data set 2).

Case	Data set	Parameters	Constraints
1	1	σ_1, σ_A, α	—
2	1	σ_1, σ_A	$\alpha = 0$
3	2	σ_1, σ_A, α, β_1, β_A, λ	—
4	2	σ_1, σ_A, α, β_1, β_A	$\lambda = 0$
5	2	σ_1, σ_A, β_1, β_A, λ	$\alpha = 0$
6	2	σ_1, σ_A, β_1, β_A	$\lambda = 0$; $\alpha = 0$

Results and discussion

Comparison of reader ages to known ages

The primary reader ages agreed with the known ages in 35.4% of the cases (Fig. 1). Of the 49 known-age sablefish otoliths, the primary reader chose not to age one specimen because of the poor condition of its otoliths. Of the 31 misaged fish, the primary reader misaged most (80.6%) by 1 year: 17 of the 18 underaged fish and 8 of the 13 overaged fish. In three cases (known ages=4, 6, and 6 years), the primary-reader ages differed substantially at 8, 11, and 12 years.

Results for the tester were generally similar to those of the primary reader. The tester age agreed with the known age in 38.6% of the 44 total otoliths that the tester aged (Fig. 1), and 5 otoliths were considered unreadable. Of the testers's misaged fish, most (70.1%) were misaged by 1 year: 10 of the 13 underaged fish and 9 of the 14 overaged fish. The largest discrepancy was 4 years: known age was 9 years and tester age was 13 years.

Agreement between primary reader and tester ages was much greater than between the known and primary-reader ages or the known and tester ages (Fig. 1). Primary reader and tester matched ages in 24 of the 44 (54.5%) specimens compared, indicating that they interpreted annuli similarly. Most discrepancies (n=12; 60.0%) were discrepancies of one year. The primary reader tended to age the fish younger than the tester: 12 less than tester ages and 8 greater. Only once did their ages differ by more than two years (known age=9; primary reader=9; tester=13).

Table 2

Comparison of parameter estimates for alternative models of ageing error for sablefish based on primary reader and tester data (data set 1) and reader and known-age data (data set 2). Number of observations (n), maximum age (A), number of parameters (N), minimum values of the inference function (l), and Akaike information criterion (AIC) are also given.

Case	Data set	n	A	N	σ_1	σ_A	α	β_1	β_A	λ	l	AIC
1	1	88	13	3	0.399	2.464	–0.358	—	—	—	139.3	145.3
2	1	88	13	2	0.270	1.094	set to 0	—	—	—	143.1	147.1
3	2	92	9	6	0.253	1.792	0.341	–0.284	0.289	0.116	308.8	320.8
4	2	92	9	5	0.213	1.796	0.346	–0.191	0.307	set to 0	308.9	318.9
5	2	92	9	5	0.911	1.948	set to 0	–1.731	0.276	0.604	310.0	320.0
6	2	92	9	4	0.699	2.089	set to 0	–0.340	0.433	set to 0	310.4	318.4

This study generally confirmed the criteria used for ageing young sablefish. Even though a high proportion of fish were misaged, most fish were misaged by only one year. In addition, after reexamining the otoliths after the known ages had been revealed, the primary reader could reconcile the differences between the known and assigned ages in most cases (25 of 31). Anderl and Heifetz[2] have described three types of misinterpretation of otolith patterns that resulted in most misages: 1) misinterpretation of an ambiguous check (i.e. false annulus) immediately following the first annulus; 2) misinterpretation in assessing whether the most recent year's annulus had been formed; and 3) misinterpretation of multiple checks on parts of the otolith (a check is a mark, growth zone, or part of a growth zone on an otolith that does not form annually but reflects various environmental or physiological changes [Chilton and Beamish, 1982]).

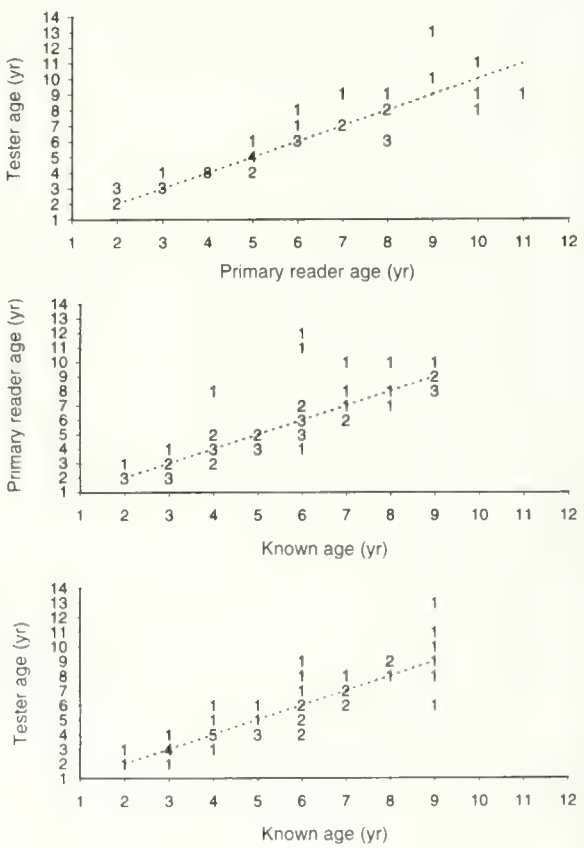

Figure 2

Observed relation for sablefish between primary reader age and tester age, known age and primary reader age, and known age and tester age. Points are represented by the frequency distribution of observations. A dotted line of slope 1 is included for reference in each panel.

Analysis of ageing errors

Table 2 summarizes the parameter estimates for various model specifications from the data in Figure 2. The estimates based on between-reader variability include only data where both primary reader and tester readings were available. The data consisted of $I = 44$ fish and $J = 2$ readings per fish resulting in $n = 88$ observations. The estimates based on reader and known ages were derived from data where at least one reader determined an age. The data consisted of $I = 44$ fish with $J = 2$ readings per fish and $I = 4$ fish with J = 1 reading per fish resulting in $n = 92$ observations.

For the estimates that included only between-reader variability, a model with all three parameters estimated (case 1) provided the best fit with the fewest parameters (i.e. lowest AIC values). The AIC value for a model with α constrained to 0 (case 2) was nearly

[2] Anderl, D., and J. Heifetz. 1999. An evaluation of ageing criteria for sablefish based on known age specimens. In prep.

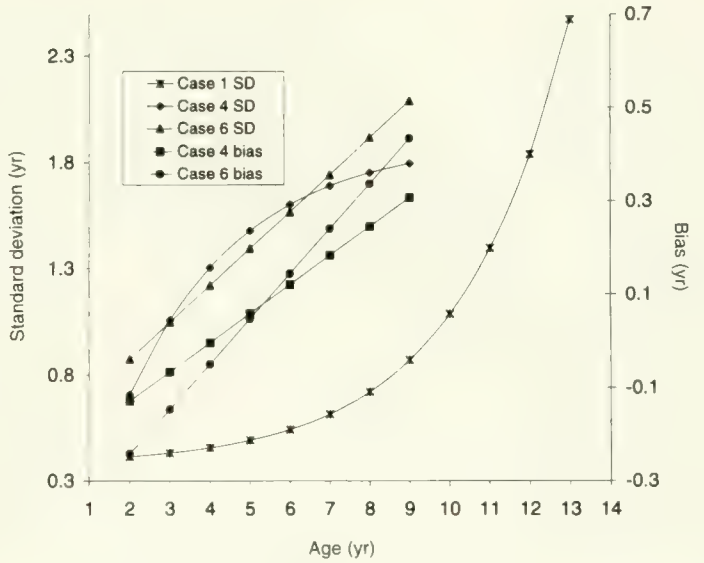

Figure 3

Estimated standard deviation (SD) and bias of observed age of sablefish for each true age based on primary-reader and tester ages (case 1) and reader and known ages (case 4 and case 6). Case refers to model specifications listed in Table 1.

2 units above the AIC value for case 1. For the reader and known-age data set, a model with α and λ constrained to 0 (case 6) provided the best fit with the fewest parameters. The AIC value for a model with only λ constrained to 0 (case 4) was only 0.5 units above the minimum. The closeness of the AIC values for these two cases indicates that case 6 provides only a slightly better model fit than case 4. The difference between case 4 and case 6 is best understood by comparing estimated standard deviation and bias at age (Fig. 3). Case 4 results in a nonlinear relationship between standard deviation and age, and the standard deviation approaches an asymptote near age 9; whereas for case 6, the standard deviation increases linearly with age. Bias is linear for both cases, and case 6 has higher absolute bias than case 4 for most ages.

Estimates of ageing errors based on comparison of known ages to reader ages were considerably higher than estimates obtained from between-reader variability (Fig. 4). For example, for age 2–9 fish, according to primary reader and tester ages, the estimates of the probability of assigning the true age was 0.95–0.46. In contrast, according to the estimates from reader and known ages, the probability was only 0.71–0.19. This discrepancy was expected because agreement between readers was considerably greater than between reader and known ages. Thus, use of between-reader agreement to assess ageing error may lead to a false sense of the true error.

In conclusion, use of ageing errors based on known-age samples may help improve stock assessment of sablefish. Future analysis of ageing errors for sablefish may require consideration of the time of year otoliths are taken because, as Anderl and Heifetz[2] have shown, ageing error may depend on the season when an age sample is taken. Precaution should be taken in extending our results to fish older than age 9. Results should be compared between stock assessments that use parameter estimates for the ageing-error matrix based on case 4 and case 6. If a sample is obtained that includes older known-age fish, the ageing-error matrix can be estimated for older fish. We expect such a sample to be available in the future as the fish tagged as juveniles by Rutecki and Varosi (1997a) continue to be recovered. For many species other than sablefish, known-age specimens are not available. For such species, variability between readers may be the only data available to assess ageing error. Such data are valuable for evaluating the precision and consistency of ageing criteria applied by different readers. Estimates derived solely from between-reader variability should be viewed as minimum estimates of ageing error.

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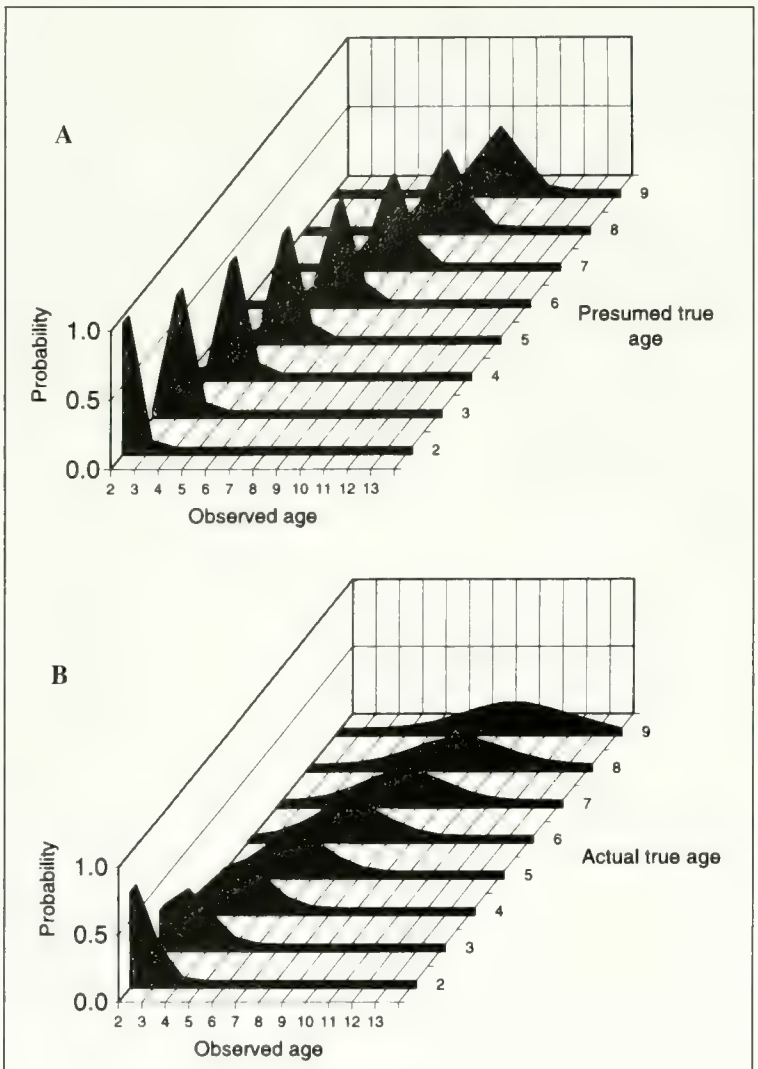

Figure 4

Estimated probability of observing a given age for a particular true age of sablefish estimated from primary-reader and tester ages (**A**, case 1) and from reader and known ages (**B**, case 6). Case refers to model specifications listed in Table 1.

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Distribution and abundance of shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, determined from a manned submersible

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Abstract.—A manned submersible was used in the eastern Gulf of Alaska in 1992 to observe spatial distributions and habitats of shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, on the continental slope at 262–365 m depths. Observations of these two species were combined because distinguishing between them was not always possible from the submersible. A seafloor area of 104,900 m^2 was surveyed at 15 dive sites, and 646 shortraker and rougheye rockfish were observed. Densities were 0.0 to 14.8 rockfish/1000 m^2 (mean, 5.8 rockfish/1000 m^2). Of the 646 rockfish, 115 were observed above bottom and 531 were on the bottom. The above-bottom rockfish were descending slowly to the seafloor and became sedentary when they contacted the seafloor. Approximately two-thirds of the rockfish were in groups; 82 of the 113 groups contained 2 or 3 rockfish, and only 2 groups had more than 12 rockfish. Rockfish were associated with 20 of the 22 substrates encountered. Soft substrates of sand or mud usually had the greatest densities of rockfish, whereas hard substrates of bedrock, cobble, or pebble usually had the least densities. Habitats containing steep slopes and numerous boulders had greater densities of rockfish than habitats with gradual slopes and few boulders; 52 rockfish lay against boulders. According to catch rates from bottom-trawl surveys, populations of shortraker and rougheye rockfish may be underestimated because of the above-bottom distribution of these rockfish and their use of steep-slope boulder habitats.

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Shortraker rockfish, *Sebastes borealis*, and rougheye rockfish, *S. aleutianus*, occur in commercial quantities from northern Washington throughout Alaska (Allen and Smith, 1988). Both species are similar in appearance and share similar life-history patterns. These rockfish attain maximum total lengths of about 100 cm (Kramer and O'Connell, 1986) and have been aged at more than 120 years (Chilton and Beamish, 1982). Their bathymetric range is 25–875 m (Allen and Smith, 1988), and their lengths at 50% maturity are 43.97 cm for rougheye rockfish and 44.90 cm for shortraker rockfish (McDermott, 1994). They apparently share similar habitats. During the 1996 Gulf of Alaska triennial survey, 89% of the trawl hauls containing shortraker rockfish also contained rougheye rockfish.

Shortraker and rougheye rockfish are harvested with bottom trawls and longlines in the Gulf of Alaska. Until the mid 1980s, they were mainly bycatch species caught during longlining for halibut, *Hippoglossus stenolepis*, and sablefish, *Anoplopoma fimbria*, and during bottom trawling for more abundant rockfish species. Before 1991, shortraker and rougheye rockfish were combined with 18 other rockfish species and managed as "slope rockfish." Since 1991, shortraker and rougheye rockfish have been managed as a separate subgroup because fishermen target these highly valued species. For example, shortraker and rougheye rockfish made up 33% of the commercial rockfish catch in the eastern Gulf of Alaska in 1990 but made up only 14% of the estimated rockfish biomass (Heifetz and Clausen, 1991). Catch quotas of shortraker and rougheye rockfish are based primarily on population estimates derived from catch rates of bottom-trawl surveys (Heifetz et al., 1996). These estimates are suspect because the catch efficiency of bottom trawls on these species is unknown and only certain types of habitats can be sampled with bottom trawls.

Catch rates from bottom-trawl surveys are converted to biomass estimates by assuming a 100% sampling efficiency for the area swept by the trawl. The area that is swept is determined as the distance between the wingtips of the net and the distance

the net is towed. The sampling efficiency could be less than 100% if fish are distributed above the headrope, protected by structures such as boulders, swim out of the path of the net, or escape under the net. Conversely, if fish are herded into the trawl by the bridles and doors and do not escape above or under the net, the sampling efficiency may be greater than 100%. Typically, smooth (trawlable) substrates are sampled during trawl surveys. Catch rates from trawlable substrates are then applied to all substrates for estimating biomass. Bottom-trawl surveys may not provide reliable biomass estimates of shortraker and rougheye rockfish because 1) the sampling efficiency may not be 100% for the distance between the wingtips of the net, 2) these species may use untrawlable substrates at a different rate than they do trawlable substrates, and 3) the sampling frequency may not be sufficient, depending on the distribution patterns of the target species.

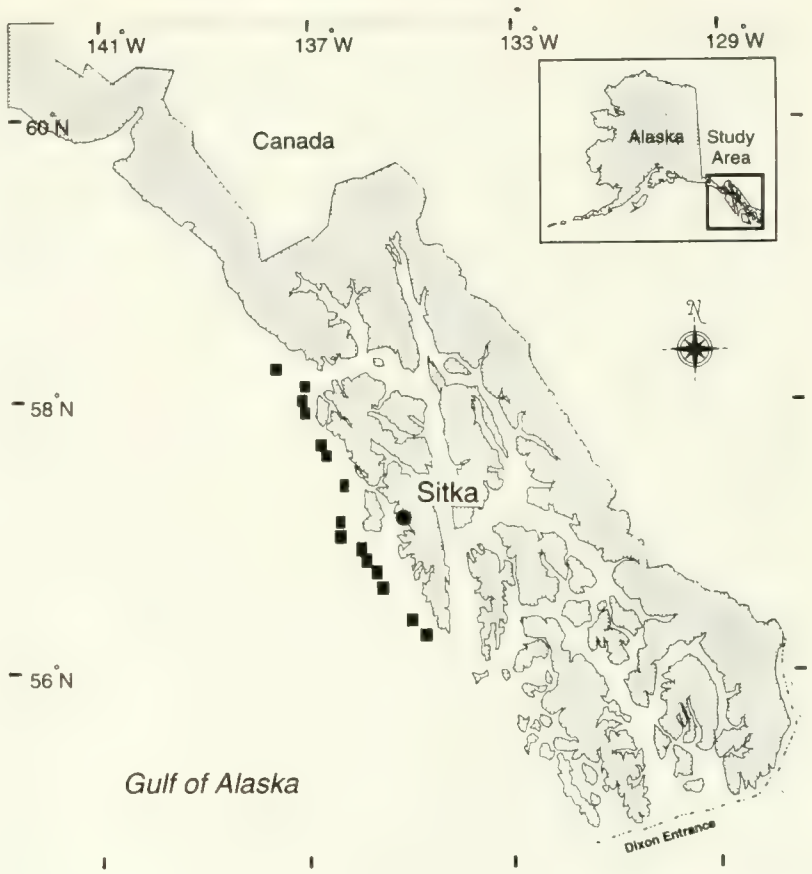

Figure 1

Submersible survey sites for shortraker and rougheye rockfish in the eastern Gulf of Alaska in May 1992.

Minimal information is available on the distribution of shortraker and rougheye rockfish. Fishermen report that rockfish school above bottom in steep-slope areas. From a manned submersible Krieger (1992) observed 20 shortraker rockfish on the continental shelf; these fish were in contact with the seafloor and were distributed as solitary individuals on shallow-sloped, smooth habitat. Shortraker rockfish were observed only at sites where boulders were common, and six of the fish were found next to boulders 0.5–1.5 m in diameter (Krieger, 1992). Catches of shortraker and rougheye rockfish during longline surveys indicate they are most abundant on the upper continental slope at 300–400 m depths (Sigler and Zenger, 1994), but most of this substrate is considered untrawlable and is seldom sampled during bottom-trawl surveys. For example, only eight trawl hauls were completed along the 500-km continental slope in southeastern Alaska during the last four bottom-trawl surveys (1987, 1990, 1993, 1996).

We need to understand the distribution and habitats of shortraker and rougheye rockfish to assess them effectively with bottom trawls or other sampling gear. In this study, a manned submersible was used to observe their spatial distributions and habitat associations. These species were also quantified from the submersible for comparison with abundance estimates from bottom-trawl surveys. The two species were combined and are referred to as rockfish in this paper because distinguishing between them was not always possible from the submersible.

Materials and methods

Study area

This study was conducted in May 1992 on the upper continental slope in the eastern Gulf of Alaska between lat. 56°10' and 58°10'N (Fig. 1). This region has consistently produced high catch rates of shortraker and rougheye rockfish during the annual longline surveys in the Gulf of Alaska (Rutecki et al., 1997). The study area spanned more than 200 km to include a variety of habitats. Distances separating adjacent sites ranged from 0.2 to 84.2 km. Dives were conducted during daylight, between 0600 and 1900 hours.

Submersible

The two-man submersible *Delta* was chartered for all dives. This battery-powered submersible is 4.7 m

long, dives to 365 m, and travels 2–6 km/h for 2–4 h. It is equipped with halogen lights, internal and external video cameras, magnetic compass, directional gyro compass, underwater telephone, and transponder that allow tracking of the submersible from a surface vessel. On each dive, the submersible descended to 265–365 m and then usually traveled parallel to the shelf break, followed by up-slope travel to less than 300 m before it ascended. The surface vessel recorded LORAN fixes at the beginning and end of a dive, and every 1–5 min during a dive. The submersible traveled 1.0–2.5 km/h, depending on the slope and ruggedness of the terrain and the magnitude and direction of the current. The degree of slope determined how observations were made from the submersible. When the slope was less than 60°, the submersible remained in contact with the seafloor while the scientist viewed the water column parallel to the seafloor through a starboard porthole 0.5 m above the base of the submersible. When the slope was greater than 60°, the submersible traveled 2–3 m away from the seafloor while the scientist viewed the water column almost perpendicular to the seafloor through portholes on the starboard side and bow. The pilot sat above the observer in a tower with a panoramic view and assisted in locating fish, especially above the submersible. The submersible lights provided constant illumination.

Data analysis

Observations of rockfish and their habitat were audiotape- and videotape-recorded for subsequent analysis and verification. The senior author reviewed all video tapes by 1-min segments (16–42 m travel distances), and four habitat parameters were estimated: 1) main substrate, 2) secondary substrate, 3) slope, and 4) boulder abundance. The main substrate made up 50–100% of the substrate, whereas the secondary substrate made up 10–50% of the substrate. Substrates consisted of mud, sand, pebble, cobble, and bedrock. Granular size used to separate pebble and cobble was 2.5 inches (64 mm), and to separate cobble and boulders was 10 inches (256 mm). Mud would stay suspended when disturbed by the submersible, whereas sand would not. Size references for classifying pebble, cobble, and boulders included the known length and width of a video frame as well as the known, uniform size of invertebrates such as sea stars and shrimp. The slope was classified into four categories: 1 = 0–5°, 2 = 6–20°, 3 = 21–45°, and 4 = 46–90°. Slope classification was based on estimates by the pilot and on the view from a downward-aimed, mounted video camera. Boulder abundance was classified into five categories: 0 = absent, 1 = scarce, 2 = scattered patches, 3 = common (usually in view), and 4 = abundant (always in view). For each site, we calculated the average slope, average boulder abundance, and the densities of rockfish associated with each substrate. For all sites combined, we calculated rockfish densities associated with each substrate, and the percentage of rockfish associated with each slope category and each boulder category.

Rockfish observations included number, size, grouping behavior, above-bottom distribution, and movements. Three sizes of rockfish were estimated visually: small (<30 cm), medium (30–60 cm), and large (>60 cm). The observers had used laser beams to measure rockfish lengths from submersibles and were, therefore, experienced in sizing them. Rockfish were considered grouped if they were within 5 m of each other. Densities were estimated from counts of rockfish and the total seafloor area surveyed. The surveyed area was the distance the submersible traveled (0.3–1.8 km/dive) multiplied by the estimated viewing distance from the submersible (4–10 m, depending on water clarity). These estimates were calibrated against sonar readouts when the seafloor became visible during descents and when the seafloor disappeared from view during ascents. Estimated distances were within 1 m of true distances according to sonar readouts and distance calibrations in previous studies (Krieger, 1993). Rockfish movement rates were based on the estimated distance moved during a specific time period.

Results

Submersible dives

Fifteen submersible dives were completed and 104,900 m^2 of seafloor was surveyed at 262–365 m depths (Table 1). Rockfish densities ranged from 1.2 to 14.8 rockfish/1000 m^2 (mean, 5.8/1000 m^2) at the 14 sites where they were observed. Of the 646 rockfish observed, 188 were small, 289 medium, and 169 large.

Above-bottom and on-the-bottom behavior

We observed 115 rockfish 1–10 m above bottom and 531 on the bottom (Table 2). Sites 5 (80 above-bottom rockfish) and 13 (19 above-bottom rockfish) accounted for 86% of the above-bottom rockfish. Above-bottom rockfish were medium-size (108 rockfish) or large (7 rockfish), and they were observed descending at less than 10 m/min without detectable movements of fins or body. They would contact the seafloor without disturbing sediments and would orient broadside to the current, which would tilt them 10–45° (Fig. 2). Currents were less than 1.0 km/h at all sites.

Table 1

Number and density of shortraker and rougheye rockfish at 15 submersible dive sites in the eastern Gulf of Alaska, 1992. Small = <30 cm; Medium = 30–60 cm; Large = >60 cm.

Site	Depth (m)	Surveyed area (1000 m^2)	Number of rockfish				Density of rockfish (no./1000 m^2)
			Total	Small	Medium	Large	
1	365–262	8.1	25	16	7	2	3.1
2	323–270	1.8	0	0	0	0	0.0
3	346–285	3.5	21	10	6	5	6.0
4	362–262	10.1	60	30	26	4	5.9
5	365–292	13.0	192	24	165	3	14.8
6	365–270	7.9	43	16	19	8	5.4
7	365–270	4.0	5	3	0	2	1.2
8	365–275	7.5	45	7	9	29	6.0
9	365–300	13.5	16	0	3	13	1.2
10	365–270	1.7	21	10	6	5	12.4
11	365–304	7.3	64	28	15	21	8.8
12	365–280	2.0	17	3	3	11	8.5
13	365–320	16.3	98	29	23	46	6.0
14	365–288	5.8	34	9	5	20	5.9
15	365–285	2.4	5	3	2	0	2.1
Totals		104.9	646	188	289	169	

Table 2

The number of shortraker and rougheye rockfish observed on the bottom, above bottom, solitary, and grouped, and their distribution by group size at 15 submersible dive sites in the eastern Gulf of Alaska, 1992.

Site	Fish on bottom	Fish above bottom	Solitary fish	No. of fish in groups	No. of groups	Group size												
						2	3	4	5	6	7	8	9	10	11	12	—	15	32
1	24	1	15	10	4	2	2												
2	0	0	0	0	0														
3	21	0	14	7	2	1			1										
4	59	1	30	30	11	6	3	1	1										
5	112	80	35	157	27	9	6	2	3	1				1	1	2		1	1
6	42	1	19	24	9	6	2			1									
7	5	0	5	0	0														
8	39	6	10	35	10	4	4			1			1						
9	15	1	9	7	3	2	1												
10	21	0	6	15	6	3	3												
11	62	2	37	27	11	8	1	2											
12	17	0	7	10	3	1		2											
13	79	19	21	77	22	13	1	3	1	1		2	1						
14	30	4	22	12	5	4		1											
15	5	0	5	0	0														
Totals	531	115	235	411	113	59	23	11	6	4	0	2	2	1	1	2		1	1

Of the 531 rockfish on the bottom, only 21 moved when passed or approached by the submersible; 5 moved 0.5–1.0 m above the seafloor and swam less than 5 m away at a speed of less than 1 km/h, and 16 moved less than 2 m along the seafloor by drifting or by slight movements of fins. The submersible drifted against several large rockfish, which did not respond as they were pushed along the seafloor.

Figure 2

Shortraker or rougheye rockfish tilted with the current while lying on the seafloor in the eastern Gulf of Alaska in May 1992. Observed from a submersible.

Spatial distribution

Of the 115 above-bottom rockfish, 106 were grouped with at least one other rockfish as they descended together to the seafloor. They contacted the seafloor within 5 m of at least one other rockfish in the group. Because these fish maintained a <5-m spacing from each other, all rockfish within 5 m of other rockfish on the seafloor were considered grouped. Twelve sites had 411 grouped fish, and 14 sites had 235 solitary fish (Table 2). Most groups were small; 82 of the 113 groups contained only 2 or 3 rockfish, whereas only two groups contained more than 12 rockfish. Twenty-six pairs of rockfish consisted of a small and medium-size fish separated by less than 0.5 m.

Substrate associations

Twenty-two combinations of primary and secondary substrates were encountered at the 15 sites (Table 3). Substrates changed frequently within each site, averaging 6.9 substrates/site. Rockfish were associated with 20 of the substrates, but no consistent pattern of association was observed within a site. For example, the 8 greatest densities (>16 rockfish/1000 m^2) included 7 different substrates, the 23 lowest densities (no rockfish) included 13 different substrates, and 3 substrates had both more than 16 rockfish/1000 m^2 and no rockfish.

For all sites combined, the most abundant substrate was cobble with sand (17.3%), whereas 7 of the 22 substrates made up 1.0% or less each of the total substrate (Table 4). The greatest densities of rockfish were usually associated with soft substrates. Sand with mud had the greatest average density (9.1 rockfish/1000 m^2), and 7 of the 10 greatest densities were associated with primary substrates of sand or mud. Nine of the 12 lowest densities of rockfish were associated with primary substrates of cobble, rock, or pebble.

Boulder and slope associations

Average boulder indices ranged from 0.0 to 2.1 (Table 3) and were not highly correlated (r=0.30) with rockfish densities. For all sites combined, high-abundance boulder habitat contained greater densities of rockfish than did low-abundance boulder habitat (Fig. 3). Habitats where boulders were absent (index=1) or rare (index=2) were encountered 67% of the time and had 56% of the rockfish, whereas habitats where boulders were more abundant (index=3, 4, or 5) were encountered 33% of the time and had 44% of the rockfish; 52 rockfish were found lying against boulders (Fig. 4). The only site without boulders (site 2) was the only site not containing rockfish.

Average slope indices ranged from 0.9 to 3.7 and were not highly correlated (r=0.56) with rockfish

Table 3

Densities of shortraker and rougheye rockfish associated with specific substrates at 15 submersible dive sites in southeastern Alaska, 1992, and indexes of boulder abundance and topography (slope). Indexes are averages of 1-min video segments, where boulders were absent (0), rare (1), scattered patches (2), common (3), or abundant (4), and slopes were 0–5° (1), 5–20° (2), 20–45° (3), or 45–90° (4). M = mud; S = sand; C = cobble; P = pebble; R = rock; M-S = mud and sand; M-C = mud and cobble, etc.

Site	Boulder index	Slope index	Rockfish densities (no./1000 m^2) and associated substrates																				
			M	M-S	M-C	M-P	M-R	S	S-M	S-C	S-P	S-R	P-S	P-M	P-C	C	C-S	C-M	C-P	C-R	R	R-S	R-M	R/P
1	1.1	2.0						3.1		3.1	2.1		4.1		3.1	3.1	2.1		2.2					
2	0.0	2.0								0.0			0.0		0.0		0.0		0.0					
3	0.7	3.0			4.0	12.8				12.0	8.0				0.0		1.0		0.0					
4	1.1	3.0	0.0	11.8		12.8	0.8		3.0	5.9	8.9		7.9	9.6			4.9							
5	1.7	2.9		5.1				22.3	70.9	9.7							16.9							
6	1.2	3.5	0.0		8.7	4.0				1.9			13.0		5.8		5.8	0.0	0.0			17.3	6.7	2.9
7	1.6	2.0									0.8		3.2	1.1					0.8					
8	2.1	2.0	3.0			0.0		6.5	6.0	6.0	7.4						0.0							
9	0.8	0.9	1.0		1.3	3.9							1.6	0.0	0.5		1.1	0.0	0.0	0.0				
10	0.4	3.7		13.7						25.1							0.0							
11	0.7	3.7		6.5	25.8	12.9				0.0	6.5		9.0		3.2		17.7		6.5					
12	1.1	3.0															11.7		7.6					
13	1.7	3.2						14.0		3.0	5.4		6.0		5.5		9.5		7.5		3.0	3.0		3.0
14	1.9	2.9								11.7	28.0	1.7				0.0	4.9					5.9		
15	1.2	2.4						0.0		4.5		0.0					4.5			0.0		4.5		

densities (Table 3). For all sites combined, habitats with slopes greater than 20° contained greater densities of rockfish than those with slopes less than 20° (Fig. 5). Slopes less than 20° were encountered 37% of the time and had 24% of the rockfish, whereas slopes greater than 20° were encountered 63% of the time and had 76% of the rockfish.

Submersible counts versus trawl catch rates

During the last four bottom-trawl surveys (1987, 1990, 1993, 1996), eight trawl hauls were completed on the continental slope in southeastern Alaska and 234,100 m^2 of seafloor was sampled. The mean catch rate was 3.2 rockfish/1000 m^2 for the 8 trawl hauls, compared with the mean observation rate of 5.8 rockfish/1000 m^2 at the 15 dive sites. Catch rates exceeded 5.0 rockfish/1000 m^2 at only 2 of the 8 trawl sites, whereas observation rates exceeded 5.0 rockfish/1000 m^2 at 10 of the 15 dive sites.

Discussion

Because the two rockfish species were combined in this study, we did not determine whether shortraker rockfish behavior differs from rougheye rockfish behavior. They appear to share the same habitats, based on bottom-trawl sampling and observations from the submersible, but differences may exist in

Table 4

The percentage of each seafloor substrate and density of shortraker and rougheye rockfish associated with each substrate observed during 15 submersible dives in southeastern Alaska, 1992.

Substrate type	Substrate (%)	Rockfish (no./1000 m^2)
sand-mud	1.0	19.1
cobble-sand	17.3	9.7
mud-cobble	1.7	9.3
sand	6.5	8.4
mud-pebble	5.0	7.0
sand-cobble	10.0	6.7
rock-mud	2.0	6.7
mud-sand	7.5	6.1
rock-sand	3.6	6.0
sand-pebble	10.5	5.5
pebble-mud	2.4	5.5
pebble-sand	11.5	3.7
cobble-pebble	7.7	3.5
rock	0.6	3.0
rock-pebble	1.0	3.0
pebble-cobble	6.0	2.5
cobble-rock	0.5	2.1
sand-rock	0.6	1.5
mud	2.1	0.9
mud-rock	1.1	0.8
cobble-mud	0.8	0.0
cobble	0.4	0.0

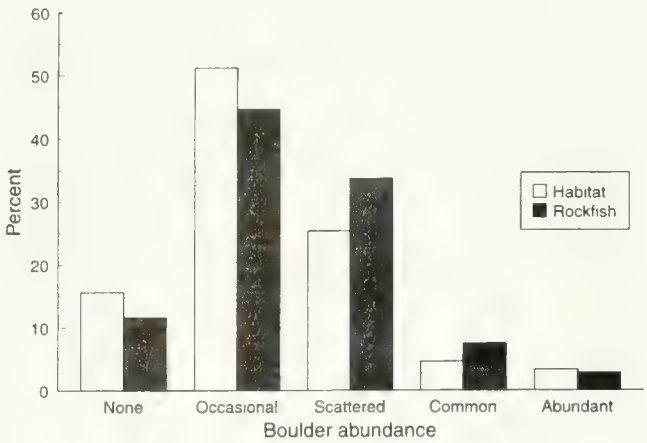

Figure 3

Five levels of boulder abundance observed on the seafloor, and the percent occurrence of habitat and percent occurrence of shortraker and rougheye rockfish associated with each level. Observations are from a submersible in the eastern Gulf of Alaska, 1992.

their above-bottom distributions, grouping behavior, and use of boulders.

The 150 rockfish observed above bottom were at nine different dive sites and all were descending, indicating they were reacting to the submersible. They were probably seeking the seafloor in response to the submersible. A diving response to trawl and vessel disturbances has been noted for other species of offshore rockfish (Kieser et al., 1992). The protection provided by the seafloor may explain their reluctance to move when they are on the seafloor and approached by the submersible. Assuming rockfish were descending in response to the submersible, the proportion of rockfish observed above bottom is probably a minimum estimate because some had probably reached the seafloor before they were viewed from the submersible. The 80 rockfish above bottom at site 5 indicate that a high percentage of rockfish move above the seafloor, although the frequency and duration of their movements are unknown. Rockfish may move above bottom to capture prey such as the squid and lantern fish (Myctophidae) on which they are known to feed (Yang, 1993, 1996). About two-thirds of the rockfish were in groups of 2–6 fish; only two groups contained more than 12 fish. The reason for the close pairing of a small and medium rockfish is unknown; it is probably not related to mating because female shortraker and rougheye rockfish shorter than 30 cm are not mature (McDermott, 1994).

The spatial distribution of rockfish varied within dive sites. This variability can be partially explained by their grouping behavior and by their habitat associations. Rockfish were associated with most of the habitats encountered, but the greatest densities were associated with soft substrates, frequent boulders, and slopes greater than 20°. Their association with soft substrates may be prey related. Pandalid shrimp and hippolytid shrimp, which concentrate on soft substrates, were the main prey of rougheye rockfish examined from the Gulf of Alaska (Yang, 1993, 1996) and from the Aleutian Islands (Yang, 1996). The association of rockfish with boulders in this study and on the continental shelf (Krieger, 1992) indicates that boulders are important for these species. Perhaps boulders are a necessary habitat feature, because shortraker and rougheye rockfish were absent at the one site without boulders in this study and at the three sites without boulders in a previous study (Krieger, 1992). These species may use boulders as territorial markers, to avoid currents, or to capture prey. Rockfish were least abundant on shallow-slope habitat (<5°) in this study, and Krieger (1992) observed shortraker rockfish at three sites where the slope was 3–12° but none at six sites with slopes less than 2°. Steep slopes may provide relief from currents.

The mean observation rate from the submersible was about twice the mean catch rate from bottom-trawl surveys, probably because of the limited habitats sampled during trawl surveys. Bottom trawling may be effective for sampling shortraker and rougheye rockfish on low-relief habitats because these rockfish descended and remained on the sea-

Figure 4

Observation from a submersible of a shortraker or rougheye rockfish lying against a boulder in the eastern Gulf of Alaska in May 1992.

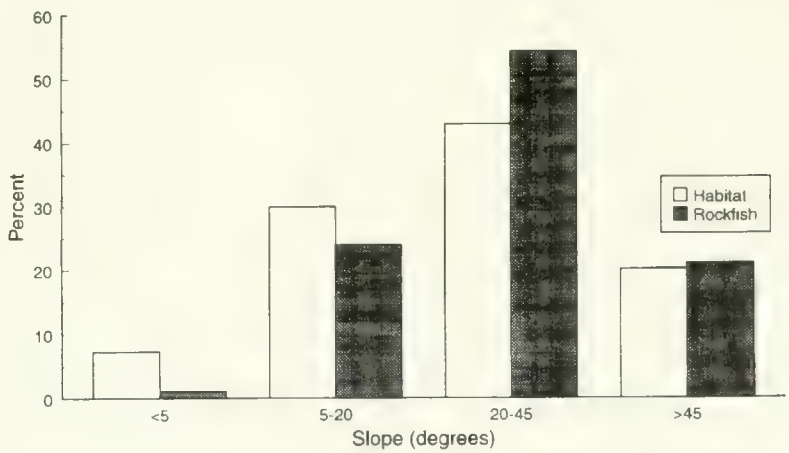

Figure 5

Four levels of slope observed on the seafloor, and the percent occurrence of habitat and percent occurrence of shortraker and rougheye rockfish associated with each level. Observations are from a submersible in the eastern Gulf of Alaska, 1992.

floor in response to the submersible. However, some above-bottom rockfish may not be captured because of their slow rates of descent. Bottom-trawl assessment gear is not designed to sample the steep-slope, boulder habitats occupied by these species, and the few trawl hauls that are completed in boulder habitat likely do not sample rockfish associated with boulders. An assessment method is needed that addresses the wide range of habitats, above-bottom distribution, and grouping behavior of shortraker and

rougheye rockfish. Longline gear and bottom trawls with large rollers can sample rugged habitat, and studies are currently underway to determine the efficiency of these gears for sampling shortraker and rougheye rockfish.

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Nutritional dynamics during embryonic development in the viviparous genus *Sebastes* and their application to the assessment of reproductive success

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Abstract.—Concentrations of lipids and protein were measured in embryos during gestation in two species of viviparous rockfishes off the central California coast. Total lipids and protein declined linearly through embryonic maturation in semipelagic yellowtail rockfish, *Sebastes flavidus*, and pelagic shortbelly rockfish, *Sebastes jordani*. Energetically, lipids were the predominant source of energy for embryonic development in both species, but lipid and protein catabolism was significantly greater for yellowtail rockfish. Total lipids, protein, and lipid class composition were measured during embryonic maturation in three populations of shortbelly rockfish, located at Ascension, Pioneer, and Bodega submarine canyons, to determine intraspecific variability of nutritional dynamics. Triacylglycerols and polar lipids (mostly phospholipids), the predominant lipid classes in all maturation stages, were depleted through embryonic development. Steryl or wax esters and cholesterol also declined, but were in much lower concentrations. The goodness-of-fit of linear regressions for protein, total lipid, and lipid classes by stage of embryonic maturation allowed estimations of their concentrations at birth, thus providing a measure of nutritional condition, or qualitative reproductive success. Analyses determined that there were significant differences in metabolism and estimated concentrations at birth of nutrients between the two species and among the shortbelly rockfish populations, indicating differential potential for survival during early planktonic life stages until favorable feeding conditions occur. Results suggest that the contribution of individual populations to the diversity of metapopulations or year classes may be influenced by the nutritional condition of larvae at birth.

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Variability of annual recruitment to marine fish stocks has been attributed to several factors, including the quantity and quality of progeny produced and the influences of environmental conditions on subsequent survival. Although either factor could be effective alone, at times they may interact. Poor reproductive success, manifested by low fecundity or unhealthy progeny, or both, occurring at times of unfavorable environmental conditions, may lead to particularly weak year classes. There is evidence that factors operating at or near the time of spawning affect year-class strength in rockfishes (genus *Sebastes*) along the west coast of North America. Year-class failures of two species of rockfish were found at the extremes of the physical environmental spectrum off the central coast of California during years of very low or very high upwelling (Ralston and Howard, 1995). The data from that investigation suggested that year-class strength of yellowtail rockfish (*Sebastes flavidus*) and blue rockfish (*Sebastes mystinus*) was related to environmental conditions and was established before the pelagic juvenile stage. Further, annual variation in fecundity does not appear to be great enough to account for the variation seen in fishery recruitment of yellowtail rockfish (Eldridge and Jarvis, 1995) or other species (Shepherd and Cushing, 1980). Thus, maternal processes contributing to the health or fitness of embryos or early larvae, in addition to the more often assessed environmental factors, may significantly influence survival and year-class strength.

The assessment of reproductive success includes the determination of both the quantity and quality of progeny because year-class strength may be influenced by the health of newborns as well as by the number produced. Although fecundity is often used as a measure of reproductive success and has been related to biological and environmental factors (Blaxter, 1969), less attention has been given to the assessment of the qualitative aspects of reproductive success. This is due, in part, to the difficulty of determining which variables or processes are valid measures of egg, embryo, or larval health. Various measures have been proposed, such as egg size (Blaxter and Hempel, 1963), histological criteria (Theilacker, 1978), and biochemical analyses, including nucleic acids (Buckley, 1984), enzyme activity (Clarke et al., 1992), and biochemical composition (reviewed by Ferron and Leggett, 1994). All have merits; however, factors such as the degree of relation-

ship to growth or survival potential, ease or cost of analysis (or both), operational feasibility, or the ability to assess adequate numbers of replicates for statistical validity often diminish their utility in routine assessments of reproductive success. Consideration of when, during egg and embryonic development, valid estimates can be made is also critical to accurate assessment of success. Ideally, evaluation at hatching or birth would provide the most accurate determination of health and survival potential, but this event is of very short duration, and obtaining enough individuals to characterize a population or species is difficult.

The nutritional status, or energy content, of embryos and larvae has a clear relationship to growth and survival potential because the amount of metabolically available energy establishes the duration of survival in the environment until adequate food becomes available. Starvation during the early stages of development has been considered a major source of mortality or reduced fitness and may contribute to fluctuations in year-class strength (May, 1974; Shepherd and Cushing, 1980; Rissik and Suthers, 1996).

Low and unstable abundance of prey typifies the environment off central California during winter and early spring (Ainley et al., 1993), the period when many species of viviparous rockfish give birth (Wyllie Echeverria, 1987). Pelagic larvae rely on endogenous nutritional reserves to supplement sparse forage until the biologically productive annual upwelling season begins, usually in late March or April (Bakun, 1975).

This study describes protein and lipid metabolism during embryonic development in two species of the viviparous genus *Sebastes*. A procedure is presented to estimate the lipid and protein composition at parturition, or birth, which provides a measure of nutritional status and thus may be related to the probability for survival at the earliest free-living stage. Nutritional status at birth is presented for yellowtail rockfish and three populations of shortbelly rockfish (*Sebastes jordani*), thereby providing comparisons between congeners occupying different ecological niches and among populations separated spatially. These data are the first documentation of lipid class composition in eggs, embryos, and larvae of a viviparous marine teleost.

Materials and methods

Female *S. flavidus* and *S. jordani* were obtained from January to March, the period of reproductive development spanning late vitellogenesis to parturition, at locations off the central California coast. Yellowtail rockfish were captured by hook-and-line at Cordell Bank (38°01'N 123°25'W), a marine bank 37 km west of Pt. Reyes, at depths ranging from 50 to 150 m. Shortbelly rockfish were collected by trawl at 150 to 200 m depth in the proximity of three submarine canyons: Bodega Canyon (ca. 38°13'N 123°22'W), Pioneer Canyon (ca. 37°24'N 122°52'W), and Ascension Canyon (ca. 37°01'N 122°25'W). Fish were held on ice for up to 12 h until examination. Morphometrics (e.g. standard length; body and liver weight) were recorded and ovaries excised, weighed, and stored at –70°C. The stage of oocyte or embryonic development was identified by microscopy according to the classification scheme of Yamada and Kusakari (1991) for *Sebastes schlegeli* (Table 1).

Table 1

Embryo maturation stages (EMS) in *Sebastes flavidus* and *Sebastes jordani*.

EMS	Description
1	Late vitellogenic or migratory nucleus oocyte
2	Formation of germ disc
3	2-celled
4	4-celled
5	8-celled
6	16-celled
7	32-celled
8	64-celled
9	Morula
10	Early blastula
11	Late blastula
12	Beginning of epiboly
13	Early gastrula
14	Late gastrula
15	Embryonic shield
16	Head fold
17	Optic vesicles
18	Somite formation begins
19	Finfold
20	Optic cups
21	Auditory placodes
22	Lens forms
23	Otoliths
24	Pectoral fins
25	Retinal pigmentation
26	Heart pumping
27	Lens transparent
28	Mouth and anus open
29	Peritoneum pigmented
30	Yolk reduction
31	Prehatching
32	Hatching
33	Hatched, preborn larva

Lipids were extracted from oocytes and embryos by the method of Bligh and Dyer (1959). Total lipids were quantified by using thin layer chromatography with flame ionization detection (TLC-FID) by an Iatroscan TH-10 Mark III (MacFarlane et al., 1990; MacFarlane et al., 1993). Lipids were separated into steryl or wax ester, triacylglycerol, nonesterified fatty acid, cholesterol, and polar lipid classes on Chromarods S-III in a solvent bath of hexane:ethyl ether:formic acid at a ratio of 246:54:0.09. Quantification of separated peaks by TLC-FID was accomplished by comparing peak areas to external standard curves for each lipid class. Cholesterol oleate, triolein, oleic acid, cholesterol, and phosphatidylcholine, purchased from Sigma Chemical Co. (St. Louis, MO), were used as standards. Total protein was estimated with the Lowry method by using a bovine serum albumin standard (Lowry et al., 1951).

Analysis of variance (ANOVA) was employed to assess variation in lipids and protein by embryo maturation stage (EMS), rockfish species, or population of shortbelly rockfish. Estimated concentrations of nutrients at parturition were obtained by linear regression. All analyses were performed with SAS statistical software (SAS Institute, Inc., 1989).

Lipids and protein data are presented as concentrations, mg/g wet weight. Changes in concentration during embryonic development represent absolute changes in the quantities of lipids and protein because ovarian mass remained statistically constant through gestation for both species. ANOVA results of the relationship between GSI [gonadosomatic index = (ovary weight/body weight) × 100] and EMS were $P = 0.242$ (F=1.396, df=59) for yellowtail rockfish and $P = 0.622$ (F=0.243, df=202) for shortbelly rockfish. During gestation, changes in organic mass of ovaries were compensated by changes in water concentration. Regression equations for ovarian water concentration by EMS were

Yellowtail rockfish ovarian water (mg/g)
= 608.5 + 8.292(*EMS*),
[df=59, F=203.7, P<0.0001, r^2=0.778]

Shortbelly rockfish ovarian water (mg/g)
= 655.2 + 6.860(*EMS*).
[df=172, F=782.6, P<0.0001, r^2=0.821]

Results and discussion

There was a progressive decline in total lipid and protein during embryogenesis in yellowtail rockfish, *Sebastes flavidus* (Fig. 1). The concentration of total lipid decreased from a mean of 149.8 mg/g in unfertilized, late vitellogenic oocytes (EMS 1) to an estimated concentration of 48.4 mg/g for fully formed, hatched larvae (EMS 33) at parturition. Although no pregnant females were caught with embryos at EMS 33, the goodness-of-fit (r^2 value) of the linear regression of lipid concentration on embryo maturation stage (Table 2) suggested that calculation of total lipid at parturition was valid (Table 3). Similarly, protein declined from 225.9 mg/g during EMS 1 to 52.1 mg/g at EMS 33 (Fig. 1; Table 3). These data indicate that yellowtail rockfish embryogenesis consumed more protein than lipid for nutritional requirements because protein concentration declined 77% during development whereas total lipids decreased 68%. From an energetic perspective, however, lipid was predominantly utilized. Using values for physiologically available energy density of 39.6 kJ/g of lipid and 20.1 kJ/g of protein (Brett and Groves, 1979), we found that the 101.4 mg lipid/g embryo depleted during embryogenesis yielded 4.02 kJ of energy, whereas the 173.8 mg protein/g embryo yielded 3.49 kJ. The predominance of lipid as an energy source for viviparous reproductive development in yellowtail rockfish has been demonstrated previously (MacFarlane et al., 1993; Norton and MacFarlane, 1995). The consumption of yolk proteins, particularly those with high molecular weights > 70 kDa, during embryonic maturation of yellowtail rock-

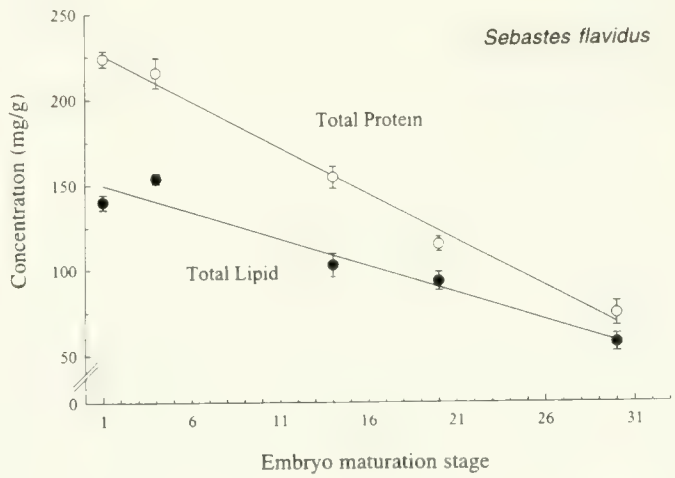

Figure 1

Total lipid and protein concentrations in oocytes and embryos by embryo maturation stage (EMS) in female yellowtail rockfish, *Sebastes flavidus*, from prefertilized oocytes (EMS 1) through the yolk-reduction stage (EMS 30). Data presented as means ± SE. Mean number (range) of females assayed at each EMS was 12 (9–17). See Table 1 for descriptions of EMS.

Table 2

Linear regression parameter estimates for mean protein and lipid concentrations in rockfish embryos in relation to embryo maturation stage (EMS). Data are for yellowtail rockfish (*Sebastes flavidus*) and three populations of shortbelly rockfish (*Sebastes jordani*) from Ascension, Pioneer, and Bodega Canyons. ND = below detection (<0.3 µg); NS = $P > 0.05$. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

Variable	r^2	Intercept ±SE	P	Slope ±SE	P
S. flavidus (n=60)					
Total lipid	0.946	153.0 ± 7.6	<0.001	−3.17 ± 0.44	<0.005
Total protein	0.993	231.3 ± 4.6	<0.0001	−5.43 ± 0.27	<0.001
S. jordani					
All canyons (n=212)					
Total lipid	0.884	89.4 ± 3.8	<0.0001	−1.86 ± 0.17	<0.0001
Total protein	0.895	167.8 ± 6.0	<0.0001	−2.85 ± 0.27	<0.0001
Esters	0.695	7.4 ± 0.5	<0.0001	−0.17 ± 0.02	<0.0001
TAG	0.917	43.0 ± 1.7	<0.0001	−0.98 ± 0.08	<0.0001
NEFA	0.141	−0.1± 0.1	NS	0.01 ± 0.00	NS
CH	0.639	3.8 ± 0.2	<0.0001	−0.05 ± 0.01	<0.0001
PL	0.889	35.4 ± 1.4	<0.0001	−0.66 ± 0.06	<0.0001
Bodega Canyon (n=49)					
Total lipid	0.699	81.0 ± 6.9	<0.0001	−1.54 ± 0.32	<0.001
Total protein	0.676	174.1 ± 14.9	<0.0001	−3.17 ± 0.69	<0.001
Esters	0.750	7.3 ± 0.6	<0.0001	−0.16 ± 0.03	<0.0001
TAG	0.704	37.4 ± 3.5	<0.0001	−0.80 ± 0.16	<0.0001
NEFA	ND	ND	ND	ND	ND
CH	0.503	3.4 ± 0.3	<0.0001	−0.04 ± 0.01	<0.01
PL	0.665	32.8 ± 2.6	<0.0001	−0.54 ± 0.12	<0.001
Pioneer Canyon (n=102)					
Total lipid	0.844	88.3 ± 4.2	<0.0001	−1.97 ± 0.18	<0.0001
Total protein	0.714	177.0 ±10.8	<0.0001	−3.29 ± 0.46	<0.0001
Esters	0.766	7.4 ± 0.5	<0.0001	−0.18 ± 0.02	<0.0001
TAG	0.835	44.6 ± 2.5	<0.0001	−1.12 ± 0.11	<0.0001
NEFA	0.284	−0.2 ± 0.1	NS	0.01 ± 0.00	<0.01
CH	0.719	3.9 ± 0.2	<0.0001	−0.06 ± 0.01	<0.001
PL	0.838	32.7 ± 1.4	<0.0001	−0.62 ± 0.06	<0.0001
Ascension Canyon (n=61)					
Total lipid	0.419	90.4 ± 8.0	<0.0001	−1.36 ± 0.41	<0.005
Total protein	0.451	165.1 ±11.8	<0.0001	−1.93 ± 0.59	<0.005
Esters	0.227	7.2 ± 1.0	<0.0001	−0.11 ± 0.05	<0.05
TAG	0.348	42.4 ± 4.6	<0.0001	−0.68 ± 0.24	<0.01
NEFA	0.072	0.1 ± 0.1	NS	0.00 ± 0.00	NS
CH	0.257	3.8 ± 0.3	<0.0001	−0.03 ± 0.01	<0.05
PL	0.520	36.9 ± 2.6	<0.0001	−0.55 ± 0.14	<0.001

fish has also been reported (MacFarlane and Bowers, 1995). Calculations of lipid and protein utilization for embryogenesis in yellowtail rockfish represent net consumption and conservative estimates because at least some maternal contributions to embryo development occur during gestation (MacFarlane and Bowers, 1995). Radio-labelled phosphatidylcholine injected into the circulatory system of pregnant females resulted in radioactivity in embryos, indicating matrotrophy for this phospholipid. The extent to which matrotrophy exists for other lipids and protein is unknown.

As in yellowtail rockfish, total lipid and protein concentrations declined linearly according to stage of development in embryos of shortbelly rockfish, *Sebastes jordani* (Fig. 2).

Embryonic development consumed 55% of the protein and 68% of the total lipid present at fertilization. Thus, both species of rockfish metabolized the same proportion of total lipids, whereas protein was conserved in shortbelly rockfish in relation to yellowtail rockfish embryogenesis. It should be noted, however, that yellowtail rockfish had significantly greater protein resources for embryogenesis at fer-

Table 3

Estimated concentrations of lipids and protein in *Sebastes flavidus* and *Sebastes jordani* larvae at birth. *S. jordani* data are for all populations combined and for each of three populations at Bodega, Pioneer, and Ascension submarine canyons. Values presented as mean ± SD in mg/g wet weight. TAG = triacylglycerols; NEFA = nonesterified fatty acids; CH = cholesterol; PL = polar lipids.

		Sebastes jordani			
Variable	*Sebastes flavidus*	All	Bodega	Pioneer	Ascension
Protein	52.1 ± 5.2	73.6 ± 6.4[1]	69.3 ±10.2	68.5 ± 6.3	101.3 ± 9.1[4]
Total lipid	48.4 ± 8.5	28.1 ± 3.7[2]	29.4 ± 4.7[3]	23.3 ± 2.7	45.7 ± 6.4[4]
Esters	—	1.9 ± 0.4	1.9 ± 0.4[3]	1.4 ± 0.3	3.8 ± 0.7[4]
TAG	—	10.5 ± 2.0	11.0 ± 2.4[3]	7.6 ± 1.6	20.1 ± 3.7[4]
NEFA	—	0.1 ± 0.1	—	0.2 ± 0.0	0.0 ± 0.1
CH	—	2.1 ± 0.1	2.0 ± 0.2	2.0 ± 0.1	2.9 ± 0.2[4]
PL	—	13.6 ± 1.4	14.5 ± 1.8[3]	12.1 ± 0.9	18.9 ± 2.1[4]

[1] Significantly greater than that for *S. flavidus* ($P<0.0001$).
[2] Significantly less than that for *S. flavidus* ($P<0.01$).
[3] Greater than that for *S. jordani* at Pioneer Canyon ($P<0.001$).
[4] Greater than that for *S. jordani* at Bodega and Pioneer Canyons ($P<0.0001$).

tilization than did shortbelly rockfish, 225.9 mg/g compared with 165.0 mg/g (Table 2). At birth, the estimated concentration of protein in shortbellly rockfish larvae was significantly greater than that in newborn yellowtail rockfish ($P<0.0001$); however, the total lipid concentration was less ($P<0.01$) (Table 3). That shortbelly rockfish have less lipid at parturition suggests they have a greater urgency for feeding than yellowtail rockfish soon after birth, or else catabolism of tissue protein would be required for maintenance, reducing the probability of survival.

Energetically, lipid was the predominant fuel for embryo development for shortbelly rockfish, as for yellowtail rockfish. The 59.4 mg lipid/g embryo metabolized between fertilization and parturition represented 2.35 kJ/g, and the 91.3 mg protein/g embryo represented 1.84 kJ/g.

Total energy consumed for embryogenesis was significantly greater in yellowtail rockfish than in shortbelly rockfish ($P<0.0001$). The production of a gram of fully formed, hatched, preborn larval yellowtail rockfish required the expenditure of 7.51 kJ of energy. For shortbelly rockfish, the equivalent energetic cost was 4.19 kJ/g of EMS-33 larvae. Because the average weight of ovaries at late stages of gestation was 204.9 ± 16.9 g (n=17) in yellowtail rockfish but only 43.4 ± 2.8 g (n=21) in shortbelly rockfish, requirements for maternally supplied nutrients were much greater for yellowtail rockfish. For comparison, the mean standard length and total weight for female yellowtail rockfish was 36 ± 0.5 cm and 1304 ± 55 g versus 21 ± 0.2 cm and 150 ± 4 g for the shortbelly rockfish assessed in this study.

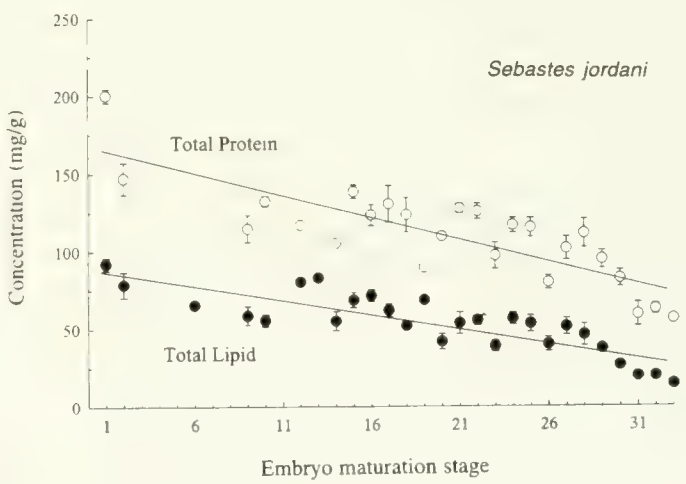

Figure 2

Total lipid and protein concentrations in oocytes and embryos in female shortbelly rockfish, *Sebastes jordani*, from prefertilized oocytes (EMS 1) through the hatched preborn larval stage (EMS 33). Data (means ± SE) from shortbelly rockfish from populations at all three submarine canyons are shown. Mean number (range) of females assayed at each EMS was 8 (1–21). See Table 1 for description of EMS.

The significant difference in energy required to produce a gram of larvae in the hatched, preborn stage in the two rockfish species may relate to differences

in reproductive strategy. Yellowtail rockfish produce about 700,000 eggs/female (Eldridge and Jarvis, 1995) whereas shortbelly rockfish fecundity is about 16,500 eggs/female (Eldridge[1]). Also, yellowtail rockfish eggs and hatched larvae are considerably smaller than those of shortbelly rockfish (Matarese et al., 1989; Eldridge[1]). Greater energy consumption for production of yellowtail rockfish larvae may be a consequence of greater energy required for the synthesis of more larvae, their organelles, and subsequent cellular differentiation.

The relative importance of lipids and protein as sources of nutrition during embryonic and larval development in oviparous fishes has been presented in other reports. In the marine teleost, *Sparus aurata*, free amino acids were the main source of energy during the relatively short embryonic period (ca. 51–58 h postfertilization) whereas lipids and protein did not supply substantial energy until after hatching (Rønnestad et al., 1994). Winter flounder (*Pseudopleuronectes americanus*), by contrast, used small amounts of carbohydrate first, then protein until hatching (Cetta and Capuzzo, 1982). Lipid depletion did not occur until after hatching. Protein concentrations were stable, whereas lipids were catabolized in eggs and newly hatched larvae of Senegal sole (*Solea senegalensis*) (Mourente and Vasquez, 1996). According to these researchers, this pattern of lipid metabolism is characteristic of temperate marine fishes with eggs containing oil globules, high lipid content, and short developmental periods. The rockfish species in the present study are temperate marine teleosts that contain oil globules and high lipid levels. However, they are viviparous and have relatively lengthy development, yet catabolize both protein and lipids for energy-consuming processes, thus emphasizing the great variability and lack of generality in the sources and patterns of nutrient use for embryonic and larval development in fishes.

Total lipid concentrations can be considered a measure of physiological condition of larvae (Ferron and Leggett, 1994), and thus an indicator of potential reproductive success, but not all types, or classes, of lipids are equivalent with respect to metabolic availability or *in vivo* energy yield. Therefore, fractionation of total lipids into classes representative of energy-yielding and structural functions provides greater knowledge of the amount of energy available to sustain growth and survival once the larvae are released into the environment.

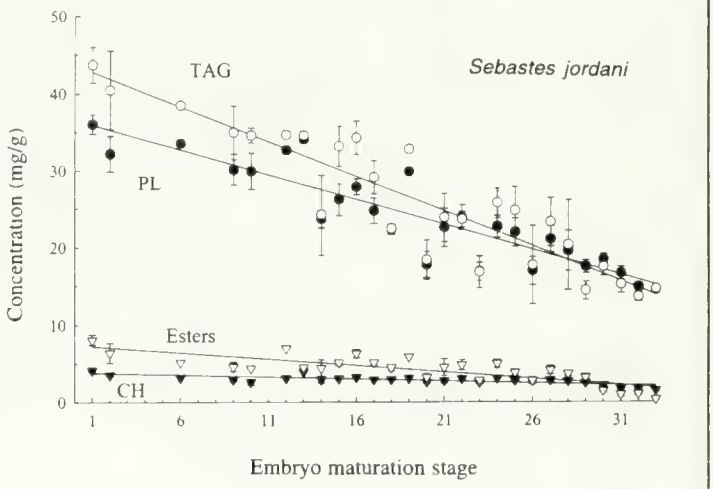

Figure 3

Changes in lipid classes during embryonic maturation in shortbelly rockfish, *Sebastes jordani*. Data (means ± SE) are from populations at all three submarine canyons. Number of females assayed for each EMS is same as in Figure 2. See Table 1 for description of EMS.

Total lipid from shortbelly rockfish embryos was fractionated into five lipid classes: steryl/wax esters (esters), triacylglycerols (TAGs), nonesterified fatty acids (NEFAs), cholesterol (CH), and polar lipids (PLs). The separations were not performed on yellowtail rockfish embryos owing to loss of samples before chromatographic analysis.

Triacylglycerols (TAGs) and PLs were the predominant lipids in all stages of embryonic maturation and showed the greatest declines during development (Fig. 3). Cholesterol (CH) and esters were found in much lower concentrations and declined slightly, but significantly, during embryogenesis (Fig. 3; Table 2). Nonesterified fatty acids (NEFAs) were found in very low concentrations and did not vary significantly by stage of maturation (Table 2).

The depletion of TAG and PL from fertilization to birth indicates the oxidation of these lipid classes for energy-requiring embryogenic processes. The use of TAG for energy storage and fuel during embryonic and larval development is well known in fishes (Boulekbache, 1981; Vetter et al., 1983; Tocher and Sargent, 1984; Fraser, 1989). Polar lipids, consisting mainly of phospholipids, such as phosphatidylcholine and phosphatidylethanolamine, although used as fundamental structural units of all biological membranes, have been shown to be a significant source of energy also for embryonic development in

[1] Eldrige, M. B. 1997. Tiburon Laboratory, Southwest Fisheries Science Center, 3150 Paradise Drive, Tiburon, CA 94720. Unpubl. data.

other fishes (Sargent, 1995). The relative contribution of TAG and PL to the energy demands of embryonic development varies by species. Whereas in cod (*Gadus morhua*) (Fraser et al., 1988; Finn et al., 1995) and Atlantic herring (*Clupea harengus*) (Tocher et al., 1985) PL was the major source of energy, in Senegal sole (Mourente and Vasquez, 1996) and gilthead sea bream (Rønnestad et al., 1994), TAG was primarily catabolized. In Atlantic salmon (*Salmo salar*), the PL phosphatidylcholine and TAG were used equally to meet energy requirements (Cowey et al., 1985).

The changes in lipid composition during embryogenesis in yellowtail and shortbelly rockfishes described here represent the first data of this kind for rockfishes or any viviparous marine teleost. The use of PL as a primary source of energy may be consistent with results from previous research revealing that phosphatidylcholine was supplied to developing embryos of yellowtail rockfish from maternal sources both before and during development (MacFarlane and Bowers, 1995). Perhaps the facility to supply phospholipids matrotrophically enhances their use as energy-yielding substrates. High concentrations of TAG in prefertilized eggs (EMS 1) and its importance as an energy source are not unexpected because both species feed heavily on euphausiids (Brodeur and Pearcy, 1984), which contain large amounts of TAG (Fricke and Oehlenschläger, 1982).

Lipid class composition has been promoted as a measure of nutritional condition for larvae of a variety of oviparous marine fish, including Atlantic cod (Lochmann et al., 1995), Atlantic herring (Fraser et al., 1987), and anchovy *Engraulis mordax* (Håkanson, 1989). Depending upon the species, the quantities of TAG or PL, or both, related to the probability for survival. Lochmann et al. (1995) suggested that survival was related to a condition index based on a discriminant function of TAG, PL, and defatted dry weight in laboratory and field-collected cod larvae. Triacylglycerol (TAG) was regarded as the critical variable in condition for herring (Fraser et al., 1987) and anchovies (Håkanson, 1989).

It is reasonable to apply this concept to the assessment of larvae from viviparous species as well. The nutritional status of larvae just prior to parturition would represent their condition at the start of life in the marine environment and would be related to their ability to survive until adequate feeding occurs. The presence of an oil globule in rockfish larvae during the early days after birth argues for the importance of lipids for energy. For rockfish, the amounts of TAG at birth should be related to survival potential because this lipid class is the predominant component in oil globules of most fishes (Henderson and Tocher, 1987; Heming and Buddington, 1988) and has consistently been shown to correlate with physiological condition (Fraser, 1989).

We analyzed embryos in pregnant female shortbelly rockfish from populations living in the proximity of three submarine canyons off the central California coast. The purpose was to determine the variability in metabolism of lipid classes for specific populations and the estimated concentrations of each lipid class at birth, thus providing a measure of nutritional status and relative probability for survival. When lipid class concentrations were assessed in embryos from the separate populations, there were differences in the amounts and rates of depletion during intraovarian development (Table 2). Two-way ANOVA determined there were significant differences among populations at the three canyons, despite being located within about a one-degree latitude span off the central California coast. All lipid classes, except NEFA, varied significantly by EMS ($P<0.0001$), population ($P<0.0001$), and the interaction of population and EMS ($P\leq0.05$).

The changes in concentrations of lipid classes were linearly related to EMS for embryos from each population (Table 2). Parameter estimates from linear regressions of each lipid class by stage of embryonic maturation revealed that rates of metabolism differed among the populations (Table 2). The greatest catabolic rates of TAG and PL were found in embryos from the Pioneer Canyon population. Rates of protein depletion were also greater in embryos from Pioneer Canyon and lowest in those from Ascension Canyon.

In conjunction with initial concentrations of protein and lipid classes at fertilization, the rates of nutrient metabolism can be used to estimate concentrations at parturition (EMS 33). The greater rates of nutrient utilization for embryos in females from the population at Pioneer Canyon resulted in the lowest levels of nutritional stores at birth of the three populations evaluated (Table 3). Conversely, newborn larvae from females at Ascension Canyon contained the greatest concentrations of lipids and protein, suggesting that they have a greater likelihood of survival until suitable feeding conditions exist.

The differential status of nutrient levels in larvae at birth may contribute to differences in survival rate among the populations and, thus, influence the diversity of the species year class. Parturition occurs during the winter when oceanic conditions prevail along the California coast. This is the period of lowest primary and secondary productivity annually (Ainley, 1990). Until marine conditions become favorable for biological productivity, usually in April

when seasonal upwelling and increasing solar radiation stimulate phytoplankton growth, larvae must subsist on the combined resources of endogenous reserves and limited prey abundance. During the days following birth, the quantity of lipid reserves may influence the length of time larvae can persist until adequate forage is available to sustain survival and growth. Starvation has been considered a factor in recruitment variability in rockfish species (Moser and Boehlert, 1991). Larvae from populations with lesser energy reserves may experience greater mortality, thereby reducing their representation in the year class for the species along the entire coast.

The use of lipid and protein data as an indicator of nutritional condition at birth for rockfish in the genus *Sebastes* marks an extension of such data to viviparous fishes for the first time. Previously, lipid class analyses have been employed for condition assessments only in oviparous fish embryos (Tocher et al., 1985; Fraser et al., 1988) and larvae (Fraser, 1989; Håkanson, 1989; Lochmann et al., 1995).

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Abstract.—Respiration rates of nonfeeding adult menhaden induced to swim against currents of various speeds in a large circular flume at 10°, 15°, and 20°C were measured in order to quantify the cost of swimming separately from total metabolic expenditure during filter feeding. Standard metabolic rates of 0.040, 0.073, and 0.087 mg O_2 / (g wet wt · h) at 10°C, 15°C, and 20°C were estimated by extrapolation of the relationship of swimming speed and metabolic rate to zero swimming speed. We determined that when menhaden filter-feed at 20°C, at the preferred swimming speed of 41.3 cm/s, filtering and specific dynamic action (SDA) account for 59% of total energetic expenditures. The cost of locomotion was only about 23% of the total expenditure. Our results are compared with routine oxygen consumption rates of larval and juvenile menhaden as a function of temperature and with extensive metabolic data for sockeye salmon.

Metabolic rate in relation to temperature and swimming speed, and the cost of filter feeding in Atlantic menhaden, *Brevoortia tyrannus*

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The Atlantic menhaden, *Brevoortia tyrannus,* is a pelagic filter-feeding clupeoid inhabiting coastal waters of North America from Maine to Florida. Menhaden adopt filter feeding in early juvenile life (Peck, 1893; June and Carlson, 1971; Friedland et al., 1984). Adults are obligate filter feeders and consume phytoplankton, zooplankton, and detritus larger than about 13 μm (Durbin and Durbin, 1975). Menhaden are size selective in their feeding, but the basis of selection is passive, reflecting the size distribution of particulate material in the water relative to the "pore size" of the gill rakers; they do not actively pursue individual prey. Energy expenditures during "ram" filter feeding (analogous to towing a plankton net) are high (Durbin et al., 1981; Sanderson and Cech, 1992), probably due to the hydrodynamic drag of the filtering apparatus. However, menhaden compensate for the high cost of filter feeding by regulating their swimming speed to maximize the ratio of net energy gain to expenditure (Durbin and Durbin, 1983), as predicted by Ware (1975). Our study was undertaken to partition the previously determined energetic cost of filter feeding (Durbin and Durbin, 1983) into two components: the cost of locomotion alone and the cost of filter feeding. This division was accomplished by measuring respiration rates of nonfeeding fish forced to swim against currents of known speed and by comparing these respiration rates with those of feeding fish.

Materials and methods

Live Atlantic menhaden, *Brevoortia tyrannis*, were collected from a commercial fish trap located in the lower West Passage of Narragansett Bay on 22 and 25 September 1989. The fish were removed from the trap with dip nets and placed in 114-L seawater-filled polyethylene garbage cans for transport to the Narragansett Bay Campus. Menhaden were randomly divided and placed with three open-flow circular fiberglass tanks, 1.7 m in diameter and 0.5 m deep, supplied with sand-filtered seawater. Acclimation to the three test temperatures (10°, 15°, and 20°C) began 5 October 1989, starting from the ambient temperature, 18°C, with a rate of change of about 1°C/d. Ambient salinities varied between 28 and 30 ppt. The fish were considered acclimated after maintenance for 30 days at the target temperature. Menhaden were fed salmon starter mash (Ziegler Bros., Inc.) at a rate of about 4.5% of dry food:live

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Table 1

Vital statistics for the experimental fish are given in the upper panel. Relationships between respiration rate (R, mg O_2/(g wet wt · h)) and swimming speed (S, cm/s or body lengths [BL/s]) are given in the lower panel. T = temperature and FL = fork length, NF = not fed for 24 h, and FF = filter feeding.

T (°C)	No. of fish in sample	FL (cm)	Wet wt (g)	Dry wt (g)
10	13	26.0 ± 0.9	327 ± 45	99.2 ± 15.6
15	13	25.5 ± 0.6	303 ± 38	92.1 ± 15.2
20	10	25.5 ± 1.2	283 ± 40	86.4 ± 12.3

T (°C)	Behavior	Regression equation	r^2	Source
10	NF	$\log_{10} R = 0.0141\ S$ (cm/s) − 1.402 $\log_{10} R = 0.3655\ S$ (BL/s) − 1.598	0.99	This study
15	NF	$\log_{10} R = 0.0095\ S$ (cm/s) − 1.139 $\log_{10} R = 0.2419\ S$ (BL/s) − 1.861	0.90	
20	NF	$\log_{10} R = 0.0086\ S$ (cm/s) − 1.061 $\log_{10} R = 0.2187\ S$ (BL/s) − 1.939	0.96	
20	FF	$\log_{10} R = 0.0271\ S$ (cm/s) − 1.446	0.84	Durbin et al. (1981)

weight/d. The acclimation tanks were cleaned daily. During the holding and experimental periods, a 12 h:12 h light:dark photoperiod was provided by overhead fluorescent lights, and sufficient current was provided to cause the fish to orient head into the current. Experiments took place 3–14 December 1989. Vital statistics for the fish are given in the top section of Table 1.

Respiration measurements were made on a small school of menhaden because studies of schooling fishes have shown that respiration rates are higher and growth rates lower in isolated fish than in those kept in groups (Skazhina, 1975; Kanda and Itazawa, 1978; see also Ross and Backman, 1992). Experiments were begun with the 15°C trials on 3 and 4 Dec., followed by the 10°C trials on 7 and 8 Dec. The 20°C trials were conducted on 14 Dec. Thirteen fish were used for the 10°C and 15°C experiments. For the 20°C trials only 10 fish were used. Digestion is rapid in menhaden (Durbin and Durbin, 1981), and metabolism quickly returns to preceding levels after a meal (Durbin et al., 1981). Thus a starvation period of 24 h was considered sufficient to remove the effect of the previous meal on metabolic-rate measurements. Handling and transfer protocols were similarly chosen to reduce bias due to stress-induced factors, such as those identified by Waring et al. (1992) in flounder and salmon.

A sealed, toroidal fiberglass flume tank (Fig. 1A), modified from Hettler (1976), was used as a respirometer. The flume (2.75 m inside diameter, 0.51 m depth, and 0.39 m wide annular swimming channel) was large enough to hold a small school of adult menhaden. The flume was painted with a white, nontoxic, polyester gel coat. Black radial stripes 5.1 cm wide, spaced 21.8 cm apart (at the inside diameter of the flume), were painted on the walls and bottom of the flume, to provide reference marks for later determination of swimming speeds and to provide visual cues for the fish to sense displacement by the flow. To produce the desired flow rates, a high-pressure, 3.7-kW, multi-stage electric pump (Fig. 1A) was connected to coils of polyethylene tubing (6 mm inside diameter) arrayed along the walls of the flume (Fig. 1B). Discharge holes were punched at an angle of about 45° downstream and 20° downward from the horizontal with a hypodermic needle along the length of tubing to form small jets creating a counterclockwise flow in the flume. A valve placed at the pump outlet (Fig. 1A) controlled the speed of water in the flume. Return water to the pump flowed through a drain line located at the bottom of the tank and thence through a bank of 4 fiber-wound cartridge filters (3 μm). An integral reservoir (12.9-L capacity) was used to replenish sample water removed during experiments. Cooling coils were installed along the inner wall of the flume and around the pump housing (Fig. 1B) to remove heat generated by the pump and to maintain a constant temperature during trials. Water temperature was monitored with a YSI Model 2100 Tele-thermometer.

Flow rates within the flume were measured with a General Oceanics Inc. flowmeter connected to a proprietary digital display. The transducer head was

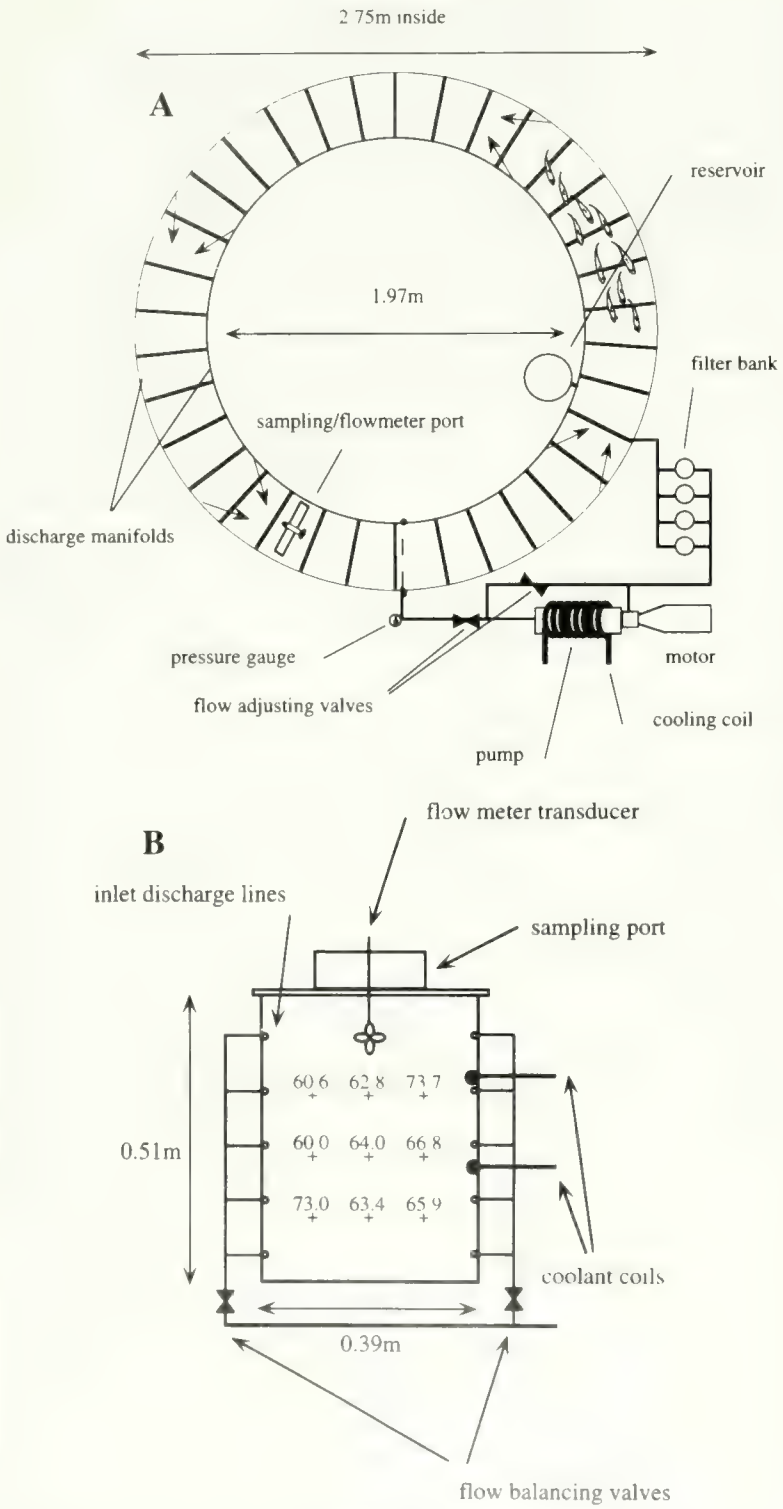

Figure 1

(**A**) Schematic view of the toroidal flume respirometer. The direction of flow is indicated by arrows within tank. (**B**) Cross-sectional view of flume tank showing arrangement of water and coolant flow. A typical cross section of the generated flow field is also shown. Speeds are cm/s. The grid spacing is 10.8 cm vertically by 8.3 cm horizontally.

suspended in the flume by a stainless steel rod (Fig. 1B). During experiments the flowmeter head was fixed radially in the middle of the flume, near the top of the water column. However, sensor depth and radial position could be varied to measure flow rate in different regions of the flume. By varying the number of discharge holes across the vertical array of inlet coils and by regulating the flow to the inner and outer inlet coils, it was possible to produce a relatively uniform cross-sectional flow field. Typical flow rates (cm/s) determined at maximum pump pressure (1.38×10^3 kPa), on a grid 10.8 cm vertically by 8.3 cm horizontally measured vertically from the flume bottom, are shown in Figure 1B. Preliminary trials established that the relationship between pressure of the inflowing water from the pump and the flow rate generated inside the flume was linear up to the maximum pump pressure, 1.38×10^3 kPa, corresponding to a flume speed of 64 cm/s. Blank trials without fish demonstrated that the system was airtight and that changes in oxygen concentration due to microbial respiration were negligible over periods comparable to those in the experiments.

Each experiment comprised a series of trials over a 2-d period. Menhaden were anesthetized with MS-222 and transferred to the flume 24 h before an experiment to permit recovery from handling stress (Barton and Schreck, 1987; Waring et al., 1992). The menhaden remained in the flume until the conclusion of the experiment and were fed in the late afternoon of each day. In the morning, fecal material and debris was siphoned off the bottom of the flume, the bottom and interior walls of the flume were scrubbed with a polyethylene scouring pad, and the flume was flushed with filtered seawater. All experiments were conducted during daylight in the afternoon, 24 h after the last feeding. The fish were accustomed to this procedure and quietly circuited the flume. A clear

Plexiglas lid, composed of interlocking sections, was then carefully fitted over the surface of the tank to provide an airtight seal. During respiration trials, the flume was operated as a closed system; between trials and at night, however, the flume received a continuous inflow of temperature-controlled filtered seawater, with a flow rate of about 6 cm/s to orient the fish.

During each 2-d experiment a series of trials was carried out at flume speeds ranging from 12–13 (minimum) to 60–63 (maximum) cm/s. Between four and six trials were conducted per day, with each trial lasting 1 h. Test speeds were selected randomly, and at the completion of a trial the next test speed was set, followed by a 30-min interval during which flow rate became stable again and fish were able to adjust to the new speed. An interval of about 1 h was used to reoxygenate the flume when necessary. Test current speeds were set by regulating the discharge pressure of the circulating pump (Fig. 1A) by using the predetermined pressure to flow-rate calibration curve. Although we attempted to use the same test current speeds at all three temperatures, minor inaccuracies in the calibration curve and gauge readings resulted in only approximately equal test speeds (Fig. 2).

Fish behavior was observed continuously during experiments and recorded with a monochrome MTI Dage M65 video camera suspended directly above the center of the flume and connected to a VHS format video recorder. Swimming speed in relation to the bottom (ground speed, GS) was determined from the video recordings at 3-min intervals, by marking the position of each fish on the video monitor screen with a grease pencil and noting its subsequent location 10 s later. The number of reference marks crossed by each fish during this interval was then multiplied by the distance between marks (21.8 cm) to obtain ground speed. Fish moving upstream were assigned positive values, whereas those swimming downstream were scored negatively. Actual swimming speed (SS) through the water was then computed as the algebraic sum of the ground speed (speed of fish in relation to the bottom) and the flow rate in the flume. Mean swimming speed during a trial was computed from the individual swimming speeds, irrespective of direction.

During experiments a YSI Model 51B dissolved oxygen meter was used to monitor oxygen levels in real time; oxygen content of the water was not permitted to decline below 60% of saturation. At 15-min intervals during a trial, duplicate water samples were siphoned from the collection port into 300-mL biological oxygen demand (BOD) bottles that were allowed to overflow twice their volume and that were then fixed for determination of oxygen content by Winkler titration (Carritt and Carpenter, 1966; Strickland and Parsons, 1972). Analyses were performed on 5–6 50 mL subsamples withdrawn from the bottles with a volumetric pipette. Dissolved oxygen declined linearly over time (overall mean $r^2 \pm 1$ SD for all regressions=0.987 ±0.018). Metabolic rates were therefore assumed to be unaffected by declining oxygen content during the trials. Menhaden respiration rates were computed from the change in dissolved oxygen content over time as determined by least squares linear regression, corrected for the wet weight of the fish and volume of the flume.

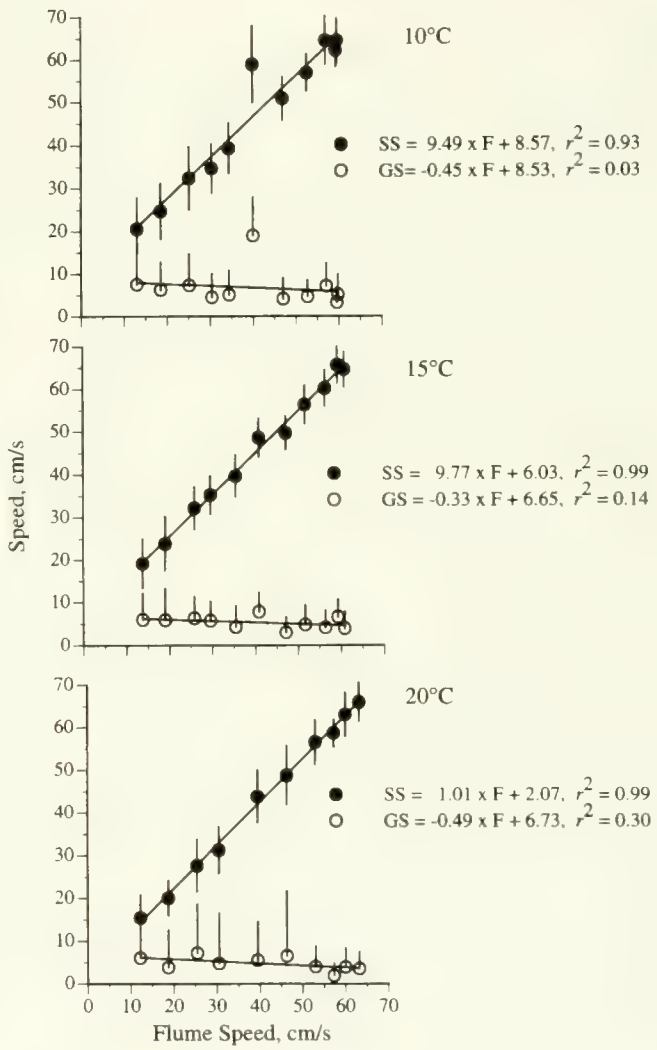

Figure 2

Ground speeds (GS) and true swimming speeds (SS) of Atlantic menhaden, *Brevoortia tyrannus*, swimming against water currents in a toroidal flume respirometer at 10°, 15°, and 20°C. Lower ground speed error bars are not shown.

Results

The menhaden formed a loose school in the upper central portion of the flume. The fish usually oriented head into the current and moved slowly upstream (positive ground speed). Occasionally a fish would break away and swim downstream with the flow, but within a few seconds reoriented itself to swim against the flow. These brief periods of downstream swimming occurred most frequently at slow current speeds and at the warmest temperature, 20°C. The frequency of occurrence of downstream coasting or swimming during respiration trials was as follows: 0 of 11 trials at 10°C; 2 of 11 at 15°C (2.2% of observations during those 2 trials); and 6 of 10 at 20°C (6.4% of observations in those 6 trials). When corrected for current speed, swimming speeds of fish moving downstream were comparable to those of fish moving upstream. Overall, the incidence of downstream swimming did not significantly affect the results.

In our study, menhaden swimming into a water current maintained a nearly constant ground speed at 10°, 15°, and 20°C (6.8, 5.3, and 4.7 cm/s respectively, or about 0.2 BL/s) (Fig. 2), whereas their true swimming speeds ranged from 20.5 to 64.6 cm/s (10°C), 19.2 to 65.7 cm/s (15°C), and 15.5 to 66.0 cm/s (20°C). The mean ground speed was not significantly different at the three temperatures ($\bar{x} \pm$ SD=6.8 ±5.8 cm/s at 10°C; 5.3 ±4.8 cm/s at 15°C; and 4.7 ±8.2 cm/s at 20°C). Because ground speed remained nearly constant, actual swimming speed increased linearly with increasing current speed in the flume (Fig. 2).

The distribution of individual swimming velocities within the school was unimodal but was skewed towards a speed slightly faster than the flow rate in the flume (Fig. 3). The coefficient of variation in swimming speed declined curvilinearly as velocity increased, indicating that fish behavior grew less variable at higher speeds (Fig. 4). The pattern of decreasing variability with increasing swimming speed was similar at all three temperatures.

Respiration rates increased exponentially with increasing swimming speed (Fig. 5, Table 1). Analysis of covariance revealed that the relationships between respiration rate and swimming speed differed significantly at the three temperatures. The regression slope, or the rate of increase in oxygen consumption per unit swimming speed, was greatest at 10°C, significantly higher than at 15° or 20°C (Fig. 6). The 15° and 20°C curves differed in elevation but not in slope, indicating that the overall level of metabolism was higher at 20°C than at 15°C, but the rate of increase in metabolic rate with increasing swimming speed was similar at the two temperatures. The cost of swimming was therefore higher at 10°C (metabolism increased by a factor of 2.32 per 1 BL increment in swimming speed) than at 15° or 20°C (metabolism increased by 1.75 and 1.65, respectively) (Table 2). At the higher test speeds, metabolic rates at 10°C were equal to or greater than those at 15°and 20° (Fig. 6).

Standard metabolism, as indicated by the y-intercepts of the equations given in Table 1, increased with temperature. At 10°, 15°, and 20°C, standard metabolism was equal to 0.040, 0.073, and 0.087 mg O_2/(g wet wt · h) respectively, or 0.131, 0.238, and 0.284 mg O_2/(g dry wt · h). The Q_{10} for standard metabolism (Prosser, 1973) was higher over the interval 10–15°C (3.3) than for 15–20°C (1.4). The Q_{10} over the interval 10–20°C was intermediate (2.2) (Table 3).

Discussion

Previous work has shown that menhaden swimming behavior reflects environmental conditions and food availability. At 20°C, adult menhaden of about 300 g swim at a characteristic speed of about 12.2 cm/s (0.5 BL/s) in still water in the absence of food (Durbin et al., 1981). During feeding, swimming speed and metabolic rate increase hyperbolically with increasing food concentration (Durbin et al., 1981). Hettler (1976) found that routine swimming speed in larval and juvenile menhaden (up to 80 g) increased with temperature but decreased with increasing salinity, starvation, and in the dark.

Ground speeds in the present experiments were remarkably stable considering the tested temperature range and the different energy expenditures at the different current speeds. The decline in individual variability in swimming speed as mean swimming speed increased (Fig. 4) was very similar to that observed by Durbin et al. (1981). This decline in variability may reflect decreased excitability as fish swim faster as well as a transition to steadier swimming with lower energy costs (reviewed in Brett and Groves, 1979; Boisclair and Tang, 1993).

The nearly constant ground speed in all trials indicated that menhaden did not approach their maximum swimming capacity at any of the tested speeds and, as a result, were probably not fatigued at the end of a day's trials despite the lack of rest between trials. The maximum observed metabolic rate of fish in our study, 0.356 mg O_2/(g wet wt · h) at 20°C, while fish were swimming at 63.2 cm/s, was considerably lower than that associated with filter feeding at a slower speed (0.538 mg O_2 /(g wet wt · h) at 20°C and 43.4 cm/s: Durbin et al., 1981), further indicating that the fish were not performing near their physiologi-

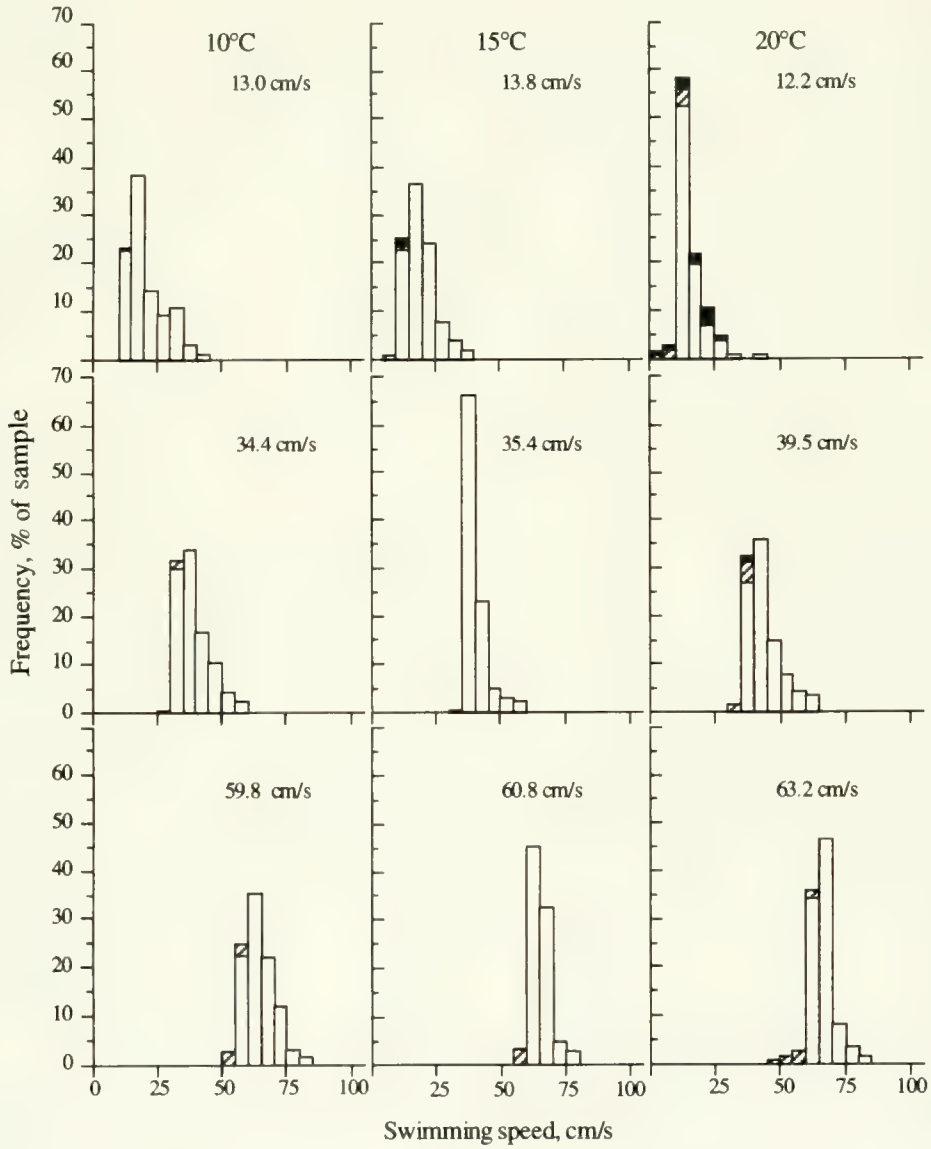

Figure 3

Frequency distribution of swimming speeds within a menhaden school swimming against typical slow, intermediate, and fast flows, at 10°, 15°, and 20°C. The flow rate inside the flume is indicated in each graph. Open bars indicate fish swimming against the current faster than the flume speed; diagonally hatched bars indicate fish swimming against the current, but slower than the flume; solid bars indicate fish actively swimming down current (i.e. with the current).

cal limit in the present experiments. Hettler (1976) measured a high oxygen consumption rate of 0.82 mg O_2/(g wet wt · h) during feeding by juvenile menhaden at 27°C, but the full metabolic scope (Fry, 1957) of menhaden remains unknown. Metabolic scope is related to the surface area of the gills and to the capacity of fish to take up oxygen from the surrounding medium. The unusually large gill area in menhaden (Gray, 1954) suggests that metabolic scope is also large.

We were unable to determine either maximum or critical swimming speeds for adult menhaden (Brett and Glass, 1973) because sufficiently high currents could not be produced in the flume respirometer. Current speeds ranged from 12 to 63 cm/s (0.5 to 2.5 BL/s), which spans the reported range of voluntary

swimming speeds during routine activity and feeding (Durbin and Durbin, 1975; Hettler 1976; Durbin et al., 1981). Swimming capacity is unusually high in Atlantic menhaden; Hartwell and Otto (1978) reported that 5.8-cm-SL juvenile menhaden sustained a critical swimming speed of 15.8 BL/s for 64 min at 20°C. The critical swimming speed of similarly sized sockeye salmon at 15°C is about 7 BL/s (Brett and Glass, 1973).

Standard metabolism (Fry, 1957) is a measure of basic maintenance costs and as such may be a useful reference level for interspecific comparisons. The magnitude of standard metabolism also seems to reflect species life styles with respect to their general activity levels. Standard metabolic rates for menhaden (Table 3) were lower than those for active predators like the bluefish, *Pomatomus saltatrix* (0.156 mg O_2/(g wet wt · h), for 217-g fish at 15°C (Freadman, 1979), but higher than those for the sedentary flatfish *Limanda limanda* (0.015, 0.029, and 0.042 mg O_2/(g wet wt · h) at 5°, 10°, and 15°C for 236–400 g fish (Duthie, 1982)). Standard metabolism in menhaden was similar to that of sockeye salmon (Brett, 1964) at 15°C, but lower at 10° and 20°C (Table 3). Durbin et al. (1981) previously estimated standard metabolism for menhaden at 20°C to be only 0.036 mg O_2 /(g wet wt · h), from the regression of feeding metabolism as a function of swimming speed. However we believe that the present higher estimates are more reliable because the data include a broader range of swimming speeds and require less extrapolation to zero swimming speed than the earlier estimate.

The Q_{10} values (Prosser, 1973) provide a measure of the effect of environmental temperature on metabolic rates. The Q_{10} for standard metabolic rate in our study was very close to that of Hettler for routine metabolism in juvenile menhaden (Table 3). The decline in Q_{10} between 10°–15°C and 15°–20°C thus appears to be real. A similar pattern was observed in dab, *Limanda limanda*, where the Q_{10} over 5°–10°C was higher than over 10°–15°C (3.7 and 2.1 respectively (Duthie, 1982). The more extensive data of Hettler (1976) and Brett (1964) indicate that over a wide temperature range (Hettler: 14–24°C; Brett: 5–24°C), the Q_{10} for metabolic rate is close to 2.0, but within this range the Q_{10} declines as the thermal optimum is approached and increases towards the thermal extremes for the species.

Hettler's data on routine metabolic rate in juvenile menhaden, when extrapolated to 300-g fish (Table 3), yield relatively high routine metabolic rates compared with those observed by Durbin et al. (1981) (0.10 mg O_2/(g wet wt · h) at 20°C). Because the maximum weight of Hettler's fish was only 74.3 g, the extrapolated values for 300-g fish are most likely overestimates. The calculated routine rates in Table 3 correspond to swimming speeds of 18.8, 25.7, and 27.4 cm/s at 10°, 15°, and 20°C, respectively, which were faster than the routine speed of 12.2 cm/s at 20°C reported by Durbin et al. (1981).

Routine metabolic rates are measured directly at spontaneous activity levels. Thus routine rates reflect real world activity levels, because few fish actually sleep or totally cease movement that would depress metabolic rates to basal or standard levels. Our present observations do seem to be comparable

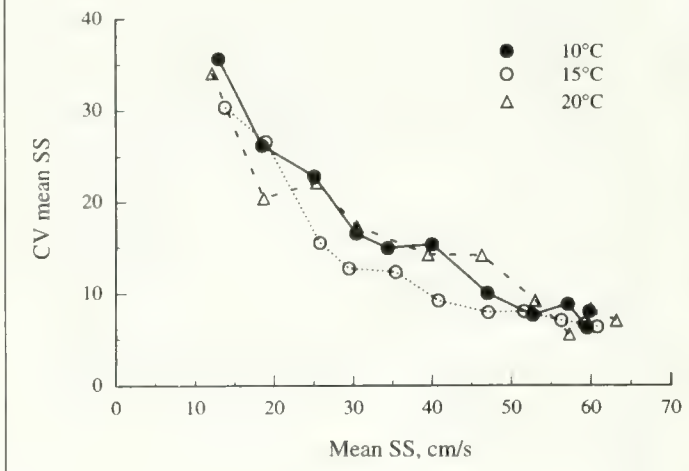

Figure 4

The coefficient of variation (CV) in relation to mean swimming speed (SS) of a menhaden school in the respirometer at 10°, 15°, and 20°C.

Table 2

Comparison of the metabolic cost of increasing swimming speed by 1 BL/sec (ratio of respiration rate at 2BL:1 BL/s) in Atlantic menhaden, *Brevoortia tyrannus* (Table 1, this study), with that in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Fish were not fed for 24 h.

	Menhaden (this study)			Sockeye (Brett, 1964)		
Temp. (°)	Length (cm)	Wt (g)	Cost	Length (cm)	Wt (g)	Cost
5				18.0	50	2.19
10	26.0	327	2.32	18.0	50	1.91
15	25.5	303	1.75	18.0	50	1.86
20	25.5	283	1.65	18.0	50	1.66
24				18.0	50	1.48

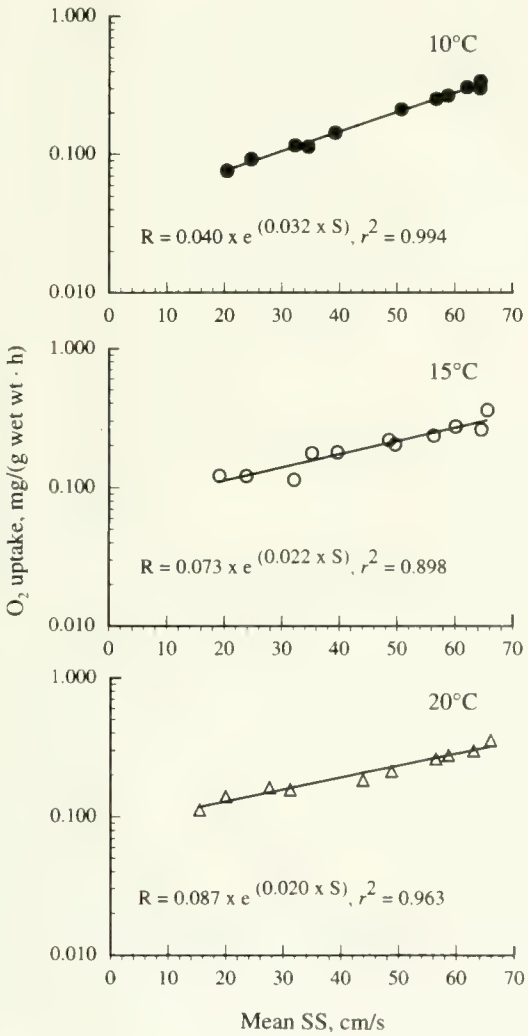

Figure 5

Relation between metabolic rate and swimming speed of fish in the respirometer at 10°, 15°, and 20°C.

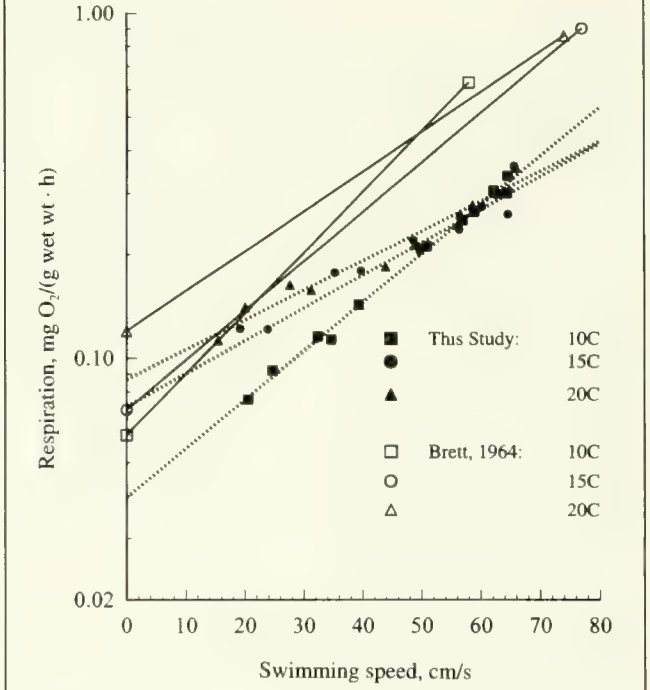

Figure 6

Comparison of respiration rate and swimming-speed relationships in menhaden (25.5–26 cm FL, 283–327 g wet wt) (Table 1, our study) and sockeye salmon, *Oncorhynchus nerka* (18 cm TL, 50 g wet wt) (Brett, 1964).

to routine rates calculated from Hettler's data (Table 3) that indicate that a 300-g menhaden at 10°C would have a routine metabolic rate of 0.073 mg O_2/(g wet wt · h) and to previously cited observations by Durbin et al. (1981) on routine swimming and metabolic rates in menhaden at 20°C. Johnstone et al. (1993) reported routine metabolic rates of 0.118 mg O_2/(g wet wt · h) for 290–380 mm Atlantic mackerel, *Scomber scombrus*, swimming at 0.6 BL/s at 11.1°C, and 0.093 mg O_2/(g wet wt · h) for 255–310 mm Atlantic herring, *Clupea harengus*, swimming at 0.3 BL/s at 9.3°C. Because these routine swimming speeds were lower than previously reported by these investigators (0.9–1.2 BL/s for mackerel, and 2 BL/s for herring) and because the fish were maintained for a prolonged period in the respirometer without feeding (5–16 d for mackerel, 13 d for herring), these may be under-estimates. Routine activity and metabolic rates in menhaden thus may be lower than in herring and mackerel.

Durbin et al. (1981) noted that the actual measured routine metabolic rate in menhaden was higher than that predicted for the same swimming speed by using the swimming-speed and metabolic-rate relationship during feeding. This higher routine rate was assumed to reflect increased excitability in fish when not occupied by feeding and also the more variable and energetically less efficient mode of swimming associated with routine activity. Routine swimming also appears to be energetically more expensive than forced swimming (as shown in our study) and directed swimming, where the optomotor response is used to induce fish to swim at a steady, but possibly more variable, speed than in forced swimming. In a review of ten species, three marine and seven freshwater, Boisclair and Tang (1993) found that routine swimming was energetically the most expensive and, on average, was 9.4 times higher (range: 6.4 to 14.0) than forced swimming at the same speed. Directed swimming ranged from 1.0 to 2.8 times as expensive. Applying a similar analysis to menhaden at

Table 3

Comparison of Q_{10} for standard (R_{Std}) and routine (R_{rout}) metabolism in Atlantic menhaden, *Brevoortia tyrannus* (this study and Hettler, 1976, respectively), with standard metabolism in sockeye salmon, *Oncorhynchus nerka* (Table II in Brett, 1964). Hettler's data were extrapolated to a 300-g menhaden by using regressions in his Table I.

	Menhaden (this study)		Menhaden (Hettler, 1976)		Sockeye (Brett, 1964)					
Temp C	Wt (g)	R_{Std} (mg O_2/(g · h))	Wt (g)	R_{Rout} (mg O_2/(g · h))	Wt C	R_{Std} (mg O_2/(g · h))	Temp C	Menhaden (this study) Q_{10}	Menhaden (Hettler, 1976) Q_{10}	Sockeye (Brett, 1964) Q_{10}
5					50	0.041				
10	327	0.040	300	0.073	50	0.060	5–10			2.2
15	303	0.073	300	0.127	50	0.071	10–15	3.3	3.0	1.4
20	283	0.087	300	0.149	50	0.120	15–20	1.4	1.4	2.9
24					50	0.195	20–24			3.4
25			300	0.231			20–25		2.4	
							5–24			2.2
							10–20	2.2	2.0	
							10–25		2.1	

20°C, we first calculated from Table 1 the metabolic rate for forced swimming at the routine speed (12.2 cm/s) = 0.111 mg O_2/(g wet wt · h) and subtracted the standard metabolic rate from Table 3 (0.087 mg O_2/(g wet w · h) to obtain the net cost of swimming = 0.024 mg O_2/(g wet wt · h). The net cost of routine swimming (Durbin et al., 1981) is 0.1 – 0.087 = 0.013 mg O_2/(g wet wt · h). The ratio of the two (= swimming cost ratio [SCR] of Boisclair and Tang, 1993) = 0.024/0.013 = 1.8. This value is much lower than Boisclair and Tang's (1993) average SCR value of 9.4 for the ratio of routine to forced swimming costs and is more comparable to their average SCR value of 1.6 for the ratio of directed to forced swimming costs. This suggests that routine activity in menhaden, although energetically more expensive than sustained swimming, is relatively economical. Metabolism associated with routine activity is, in fact, only slightly elevated above standard metabolism in menhaden. Menhaden thus may be an exception to the rule (Webb, 1991) which states that routine metabolic rates of swimming menhaden are not quasi-steady but are substantially higher than forced-swimming rates.

The cost of swimming in menhaden increases exponentially with a linear increase in swimming speed (Fig. 5, this study; Durbin et al., 1981), a pattern characteristic of fish in general (reviewed by Brett and Groves, 1979). The relation between the metabolic cost of swimming and temperature is similar for unfed Atlantic menhaden and sockeye salmon (*Oncorhynchus nerka*) (Fig. 6; Table 2). In both species, the rate of increase in respiration rate per increment of swimming speed is highest at the lowest temperature. With increasing temperature the slopes of the relationships decrease, indicating that the metabolic cost of swimming declines. The cost of swimming to unfed Atlantic menhaden is close to Beamish's (1978) mean value for eight species, where metabolism increased by 2.3-fold for a 1 BL/s increase in swimming speed. Thus we conclude that the metabolic cost of swimming in nonfeeding menhaden is similar to that of other pelagic fish species.

Conversely, the cost of swimming to menhaden while filter-feeding is much higher, where the metabolic rate rose five-fold per BL/s increase in swimming speed (Eq. 2 in Table 2, Durbin et al., 1981), compared with a 1.65-fold increase in unfed fish at 20°C (Table 2, our study). Durbin et al. (1981) speculated that the very high cost of swimming during filter feeding was related to the increased hydrodynamic drag of the expanded gill opercula and the long gill rakers that strain plankton from the water. Present results permit the separation of metabolic rate during feeding into its component parts at 20°C (Table 4; Fig. 7). We observed that during filter feeding, menhaden swam at a preferred speed of about 41.3 cm/s over a wide range of plankton concentrations. However, after prey concentrations had been reduced to subthreshold levels, feeding ceased and activity and respiration both returned to routine levels where there was no postfeeding respiration peak (Durbin et al., 1981). Standard metabolism accounted for only 18.1% of the total metabolism, and the energy demand for swimming was about 22.9%. The remaining 59% of metabolism was associated with the energy cost of feeding, which includes the in-

creased drag of the filtration apparatus, and the metabolic cost of processing the food (specific dynamic action [SDA]). SDA could not be distinguished from total metabolism during feeding (Durbin et al., 1981) because food is processed very rapidly as was shown by the fact that 50% of nitrogen was excreted 1.4 h after ingestion (Durbin and Durbin, 1981) and by the lack of a postfeeding respiration peak. The high cost of filter feeding in the menhaden provides an interesting contrast with a sedentary, ambush predator such as the Northern pike, where the energy required for prey capture is relatively small and where most of the cost of feeding is associated with SDA during an extended postfeeding period of digestion (Lucas et al., 1991).

Table 4

Partitioning of metabolism during filter feeding in Atlantic menhaden *Brevoortia tyrannus*, swimming at their preferred speed of 41.3 cm/s at 20°C. Components of the energy budget: total metabolism during feeding (R_{Feed}); total metabolism nonfeeding but swimming at the same speed ($R_{Nonfeed}$); standard metabolism (R_{Std}); metabolism associated with swimming (R_{Swim}); metabolism associated with filter feeding (R_{Filter}); metabolism associated with digestion and transformation of the food (R_{SDA}). R_{Feed} from Durbin et al. (1981); remaining data from this study.

Metabolic budget	mg O_2/(g wet wt · h)	Percent of total
$R_{Feed} = R_{Std} + R_{Swim} + R_{Filter} + R_{SDA}$	0.480	100
$R_{Nonfeed} = R_{Std} + R_{Swim}$	0.197	
R_{Std}	0.087	18.1
$R_{Swim} = R_{Nonfeed} - R_{Std}$	0.110	22.9
$R_{Filter} + R_{SDA} = R_{Feed} - R_{Std} - R_{Swim}$	0.283	59.0

The bioenergetics of feeding differ between filter feeders, such as menhaden, and particulate feeders that consume zooplankton by individual capture. Prey consumption increases linearly with prey concentration and predator swimming speed for filter feeders but increases hyperbolically (Durbin, 1979) for particulate feeders because of the limitations of handling time. The energy cost is higher for filter feeding than for particulate feeding. Both feeding modes are energetically more expensive than routine swimming (James and Probyn, 1989). The optimal swimming patterns in relation to food concentration and foraging time therefore differ between filter and particulate feeders (Ware, 1975; Durbin and Durbin, 1983). Many planktivorous fishes switch between filter and particulate feeding, according to the size and concentration of prey in the water (northern anchovy: Leong and O'Connell, 1969; O'Connell, 1972; Hunter and Dorr, 1982; cape anchovy: James and Probyn, 1989; pilchard: van der Lingen, 1994; Pacific mackerel: O'Connell and Zweifel, 1972; Atlantic herring: Gibson and Ezzi, 1985, 1990, 1992). The switch between filter and particulate feeding can be predicted from the relationship between energy gain and expenditure as the plankton size spectrum changes (Crowder, 1985; James et al., 1989; Gibson and Ezzi, 1992). In contrast, Atlantic menhaden are less flexible in their feeding behavior and consequently may be restricted to coastal and estuarine waters of high production because energetic costs of filter feeding are high and because a relatively small volume of water is searched with mode of feeding (Durbin and Durbin, 1983).

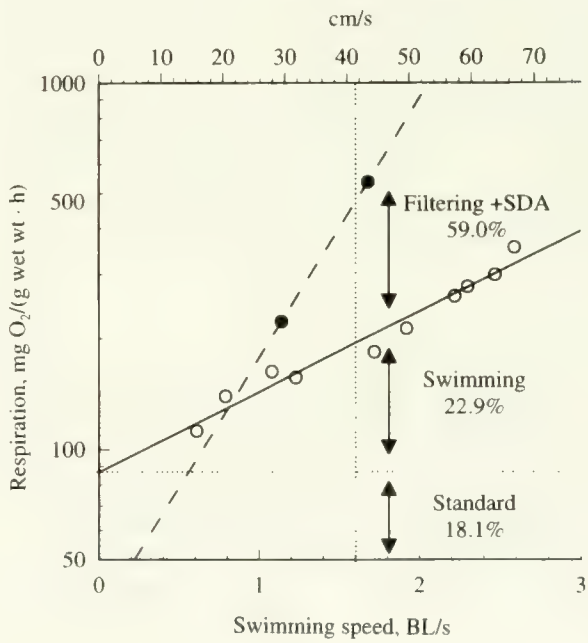

Figure 7

The energy budget of Atlantic menhaden during foraging at the preferred swimming speed, 41.3 cm/s (Durbin et al., 1981) partitioned by the vertical dotted line into the energy required for standard metabolism (horizontal dotted line), swimming (solid line), and feeding (dashed line) = filtering + SDA.

However, menhaden flourish in their chosen habitat, and as omnivores specializing in the smaller size spectrum of particulate material, they have no important competitors among the fishes. Herring and mackerel eat larger zooplankton and live further offshore. The small anchovies that live in the men-

haden's range are exclusively zooplanktivores (Bigelow and Schroeder, 1953). Mesozooplankton are competitors for both food and prey of the menhaden (Peck, 1893; Durbin and Durbin, 1975). Menhaden are important in nearshore food webs as primary herbivores and are a major prey species for predatory fishes (Bigelow and Schroeder, 1953; Friedland et al., 1989; Baird and Ulanowicz, 1989); because of their great abundance, they support one of the largest domestic finfisheries in the United States (Ahrenholz et al., 1987).

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The relation between otolith size and larval size at hatching for Atlantic cod, *Gadus morhua**

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Abstract.—We examined the relationship between otolith size and larval standard length (SL) at hatching for Atlantic cod, *Gadus morhua*, on the Scotian Shelf. We found a weak correlation between SL and area-based and radius-based measures of size of both lapillar and sagittal otoliths. Correlations of SL with the area of the lapillus were strongest. However, the predictive ability of all relationships was low. For example, the range of predicted SL at hatching of larvae with lapilli of average area included more than 90% of observed SLs in newly hatched larvae from the Scotian Shelf collected over two spawning seasons. These results suggest that otolith-based attempts to backcalculate the size of cod larvae may be prone to substantial error if sizes of particularly young larvae are estimated. We recommend that, where possible, stock- and season-specific estimates of the relationship between the area of the lapillus and larval size at hatching be used in back-calculation techniques.

The variation in year-class strength in fish populations has profound implications for our ability to manage stocks wisely. Recently, considerable effort has been focused on trying to understand why the few individuals that survive do so, rather than why the majority die (Crowder et al., 1992). This approach, which relies inherently on characterizing traits in individual fish, has been widely applied in both marine and freshwater studies (Herman et al., 1996; Rice et al., 1997 for example). The philosophy behind the approach is that by understanding how survivors differ from those that die, one may expose the mechanisms that regulate recruitment (Fritz et al., 1990).

We used this approach to explore recruitment mechanisms in Atlantic cod, *Gadus morhua*, on the Scotian Shelf. In this area, cod spawning is bimodal, beginning in late October and continuing to the following April, with peaks in December and March (Miller et al., 1995). Recent studies have suggested the importance of small-scale physical oceanographic features, such as gyres and fronts, for larval survival (Taggart et al., 1996; Lochmann et al., 1997). Abundant populations of copepods, particularly *Pseudocalanus* and *Paracalanus*, co-occur with cod larvae (McLaren and Avendaño, 1995) and support rapid larval growth. By following birth-date cohorts through time and repeatedly estimating the distribution of phenotypic and genotypic traits in the cohort, we hoped to quantify whether survivors were different functionally from the majority that died, or whether they were simply lucky (Miller, 1997).

Genetic evidence suggests that cod larvae collected on the Scotian Shelf originate from distinct spawning events (Ruzzante et al., 1996). However, Ruzzante et al. (1996) have shown that the genetic structure within the population remains stable over time. Meekan and Fortier (1996) repeatedly sampled two autumn-spawned cohorts of Scotian Shelf cod, following each for approximately six months. The pattern of survival for the two cohorts differed. In 1991–92, the growth rate distribution of survivors differed little from the growth distribution of the cohort from which they were drawn. In contrast, in 1992–93, Meekan and Fortier (1996) found evidence of strong selection

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for faster growing fish. Moreover, after comparing otolith sizes at hatching, Meekan and Fortier (1996) suggested that the potential for faster growth expressed by the survivors may have been present at hatching.

Our ability to detect examples of phenotypic selection evidenced above depends on our ability to quantify the distribution of traits in the entire cohort and to hindcast the distribution of traits in the survivors (Miller, 1997). For much of the research discussed above, and for many other individual-based studies, otolith microstructural analysis is used to detect phenotypic selection. However, to apply this approach, three requirements must be satisfied (Francis, 1990): 1) primary increments must be deposited at a known and consistent rate; 2) there must be a quantifiable relationship between growth and the width of increment rings; and 3) the initial otolith size, defined by the presence of a check mark, must be related to the size of the fish at the formation of the check.

For cod, the regularity of increment deposition has been verified and validated (Bergstad, 1984; Radtke, 1984; and see Geffen, 1995, for a recent example). Thus, the first condition for back calculation has been satisfied in cod. However, there remains considerable uncertainty over the status of the remaining two conditions. The relationship between somatic and otolith growth in cod is unclear (see Geffen, 1995, and Meekan, 1997, for opposing views). The lack of a clear relationship between rates of somatic and otolith growth may result from the natural variability among and within many cod populations (Brander, 1994; Chambers, 1997). Typcially, cod larvae grow at highly variable rates, and somatic and otolith growth may become disassociated (Suthers et al., 1989; Campana and Hurley, 1989; Geffen, 1995). Concerns over the validity of the assumed relationship between fish and otolith size at hatching also arises because of inter- and intrapopulation variation. Considerable variation has been reported in larval size at hatching both within and among populations (Bolz and Lough, 1983; Bergstad, 1984; Radtke, 1984; Knutsen and Tilseth, 1985; Miller et al., 1995). Currently, no clear link between otolith size and larval size at hatching has been established for any population.

The objective of this paper is to examine the relationship between otolith size at hatching and larval size at hatching for cod. Specifically, we address whether otolith size at hatching is significantly correlated with larval size at hatching, and whether all otoliths provide an equally accurate and precise estimate of larval size at hatching. We use data collected for cod on the Scotian shelf collected between 1991–93 to address these questions.

Methods

Sampling was carried out during 29 cruises on the Scotian Shelf between March 1991 and May 1993 (Fig. 1). O'Boyle et al. (1984) have given a general description of the Scotian Shelf system. Full details of the sampling method are given by Miller et al. (1995). We summarize the general sampling design here and provide additional details that relate to the specific objectives of this study.

Twenty six cruises were designed to provide broad-scale information on temporal and spatial distributions and abundance of cod eggs, larvae, and juveniles (Fig. 1). We sampled a rectangular grid of 45

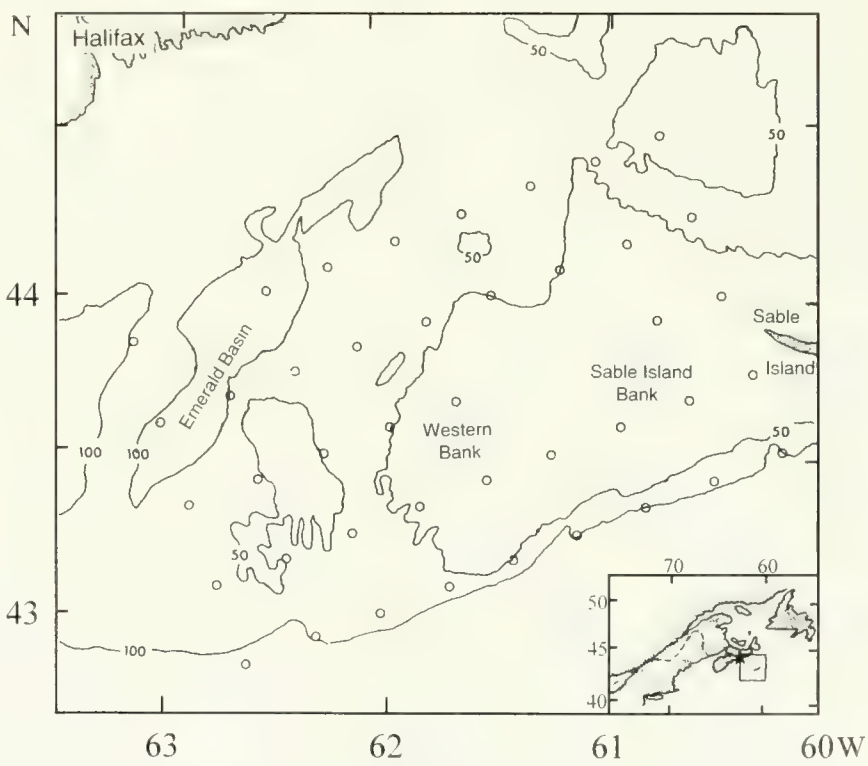

Figure 1

Map of Scotian Shelf showing the area of sampling locations. Shown on the figure are the 50- and 100-m depth contours, the principal sampling locations within the 45-station grid (open circles), and the location of Halifax, NS, Canada, for reference.

stations at roughly monthly intervals using either paired 0.61-m bongo nets fitted with 333-μm mesh nets, an 8 + 2 m rectangular mid-water trawl (RMT) fitted with 1600-μm and 333-μm mesh nets, or a paired 1.4 m^2 rectangular frame net, fitted with 333-μm mesh nets. Depth information for both the bongo and frame net was estimated from cable angles and lengths deployed. The RMT was fully equipped and provided continuous, real time depth, temperature, salinity, and volume filtered data. The station exhibiting the highest concentration of cod larvae was resampled with a BIONESS sampler equipped with ten 1-m^2, 333-μm mesh nets, that was deployed to sample discrete 5-m depth strata in the upper 25 m of the water column and 10-m depth strata at deeper depths. Three of the 29 cruises were designed to track a patch of eggs and larvae over smaller spatial scales for up to 20 days in order to track how traits changed over time. On these cruises we deployed principally a BIONESS sampler and bongo nets. However, because we were attempting to sample continuously from the same patch of water, stations were distributed irregularly in space.

All net samples were sorted and cod eggs were removed on board ship. Late-stage eggs that appeared healthy and undamaged by the collection process were videotaped under a dissecting microscope at 6–50× magnification. Individual eggs were incubated separately on a 12-h light:12-h dark cycle and at near-ambient temperature. Light from blue incandescent bulbs mimicked the light environment at depth. Nursery temperatures were recorded daily. All eggs from the same cruise were incubated at the same temperature. However, because sea temperatures varied across the sampling grid, and with depth, there were unavoidable differences between incubation and ambient temperatures for individual eggs. Vials were checked every 12 hours for hatching. When a larva hatched, it was immediately videotaped and stored in liquid nitrogen prior to otolith extraction and analysis.

In the laboratory, lapillar and sagittal otoliths were removed from larvae and mounted in cyanoacrylic cement. In most larvae we could remove and classify successfully all four otoliths. Otoliths were examined under bright field illumination under a compound microscope at 60–1000× magnification. Oil immersion was required for the higher magnifications.

Videotape recordings and otolith images were analyzed in the laboratory by using an image analysis system (Optimas v3.11, Bioscan Corporation, Seattle WA). We staged each egg according to Thompson and Riley's (1981) system. Egg diameters were calculated from three digitized points on the circumferences of eggs. From these points the diameter was calculated as

$$Diameter = \frac{abc}{4\sqrt{s(s-a)(s-b)(s-c)}},$$

where a, b, and c = the lengths of the chords connecting the three points; and

$s = 2(a + b + c)$.

Larvae that hatched from these eggs were measured to standard length (SL). Only undamaged otoliths were analyzed. Several measures were taken to describe otolith size. At this early stage, otoliths were essentially spherical in cross section. We measured the cross-sectioned area of both lapillar and sagittal otoliths. We also measured the radius of the otolith at hatching because this is the most common measurement used when estimating larval hatching sizes from otolith data.

Analysis of the data collected depended upon the purpose to which the analysis was being put. For univariate analyses to determine seasonal trends in a trait, data were aggregated to provide a mean value for each deployment before analysis. This approach reflects the sampling design employed in the field, and thus the deployment is the appropriate sampling unit. However, for bivariate analyses to determine the correlation among measures of otolith size and between otolith size and fish size, the individual fish is the appropriate sampling unit, and thus these analyses were conducted at the individual level.

Results

We identified and incubated 650 cod eggs from April 1991 to May 1993. Of this total, 259 (39.9%) successfully hatched. Otoliths from a random sample of 73 of these larvae were used in our analyses. We obtained reliable measurements from both lapilli on 56 larvae (76.7%) and from both sagittae for 59 (80.1%) larvae. The distribution of data, by month and year, is given in Table 1.

We examined the correlation structure in the data for area of otolith and radius of otolith at hatching. Estimates of otolith area were correlated among otolith types, but there were no significant correlations among otoliths from the same side of the body (Fig. 2). Moreover, the correlation among lapilli was greater than that for sagittae (Fig. 2). An identical pattern was found with respect to radius of otolith at hatching (Fig. 3).

We regressed each measure of otolith size on larval size at hatching, using only otoliths from the left side of the body. The area of the lapillus (LA) and SL at hatching were significantly and positively related (Fig 4A). Overall, longer larvae have bigger lapilli. The 95% CIs around the predicted mean were nar-

Table 1

Mean size (±SD) and number of newly hatched cod larvae from the Scotian Shelf providing data for otolith analysis by month and year. Otolith mean and SDs are calculated by using estimates for both otoliths of the specified type within each fish. Shown for each entry are the mean (upper number), SD (middle number in parentheses), and number of fish providing data for analyses (lower number).

	1991–92				1992–93			
Measurement	Nov	Dec	Jan	Mar	Oct	Dec	Mar	Total
Egg diameter (mm)	1.35	1.45	1.35	1.51	1.38	1.51	1.59	1.47
	(0.1)	(0.07)	(0.05)	(0.1)	(0.06)	(0.06)	(0.09)	(0.1)
	43	37	11	2	91	40	35	259
SL at hatching (mm)	4.31	4.43	5.04	5.34	4.03	4.52	5.03	4.38
	(0.2)	(0.3)	(0.2)	(0.3)	(0.3)	(0.3)	(0.3)	(0.5)
	43	37	11	2	91	40	35	259
Lapillar area (μm^2)	493.0	529.5	696.49	732	360.69	562.51	584.48	537.34
	(113.9)	(66.1)	(98.5)		(74.0)	(113.2)	(90.5)	(131.6)
	6	7	5	1	10	8	19	56
Lapillar radius at hatching (μm)	13.6	14.12	15.87	15.87	11.71	14.80	14.74	14.13
	(1.4)	(0.8)	(1.1)	(0.9)	(1.2)	(1.0)	(1.6)	
	6	7	5	1	10	8	19	56
Sagittal area (μm^2)	191.3	270.29	369.12	360.57	227.25	333.37	280.71	276.6
	(69.6)	(83.1)	(108.6)	(50.9)	(84.9)	(64.1)	(85.9)	
	6	11	5	1	10	8	18	59
Sagittal radius at hatching (μm)	8.79	10.39	11.98	11.85	9.55	11.32	10.64	10.45
	(1.29)	(1.4)	(1.7)	(1.2)	(1.5)	(1.3)	(1.5)	
	6	11	5	1	10	8	19	60

row. For a lapillus of average area, the predicted mean larval SL at hatching was 4.55 mm. The 95% CIs around this value were 4.4 mm < SL < 4.66 mm, a range of 0.2 mm. However, in our application we were more interested in the 95% CIs of an individual prediction. The range in these values was much wider, 3.66 mm < SL < 5.41 mm., a range of 1.75 mm. We conducted a similar analysis for the radius of the lapillus at hatching (LR, Fig 4B), which was significantly and positively related to SL at hatching. Overall, longer larvae had wide lapilli at hatching. As with the results for the total area of the lapillus, the 95% CIs for larval SL predicted for a lapillus of average radius were narrow. For a lapillus of average radius at hatching (14.15 μm), the associated 95% CIs of the mean were 4.44 < SL < 4.69 mm, a range of 0.25 mm. However, the prediction is less precise for individual back calculations for the associated 95% CIs of the individual prediction were 3.72 < SL < 5.49 mm, a range of 1.77 mm.

We conducted a similar regression analysis for the area and radius of the sagittae and SL at hatching. There were significant linear relationships for both measures of otolith size and SL at hatching (Fig. 5). For an average sagittal area of 276 μm, the predicted SL at hatching was the same as that for the lapillus. The 95% CIs for the population average were 4.38 mm < SL < 4.75, a range of 0.37 mm. The wider confidence intervals for the population mean for the sagittal measurements compared with the lapillar measurements reflected the lower coefficient of determination (r^2) of the regression. Moreover, the 95% CIs of an individual prediction, based upon sagittal area, were also wider than those for lapillus-based predictions (3.48 < SL < 5.64, a range of 2.16 mm). Similar patterns were observed for the regressions for sagittal radius at hatching (Fig. 5B).

We examined the potential for egg size and temperature to increase the predictive power of the relationships. We performed these analyses on data aggregated to the deployment level. Standard length at hatching was positively related to egg size: SL = 0.656 (±0.46) + 2.55 (±0.31) × egg diameter, n = 128, r^2 = 0.345, P = 0.0001. To explore the potential for egg size to explain additional variation in otolith-size and SL-at-hatching models, we regressed the residuals from the relationship of egg diameter to SL on several measures of otolith size. If egg size explains additional variation, independent of SL at hatching, we would expect to see a significant regression statistic. The residuals were significantly related to the area and the radius at hatching of the

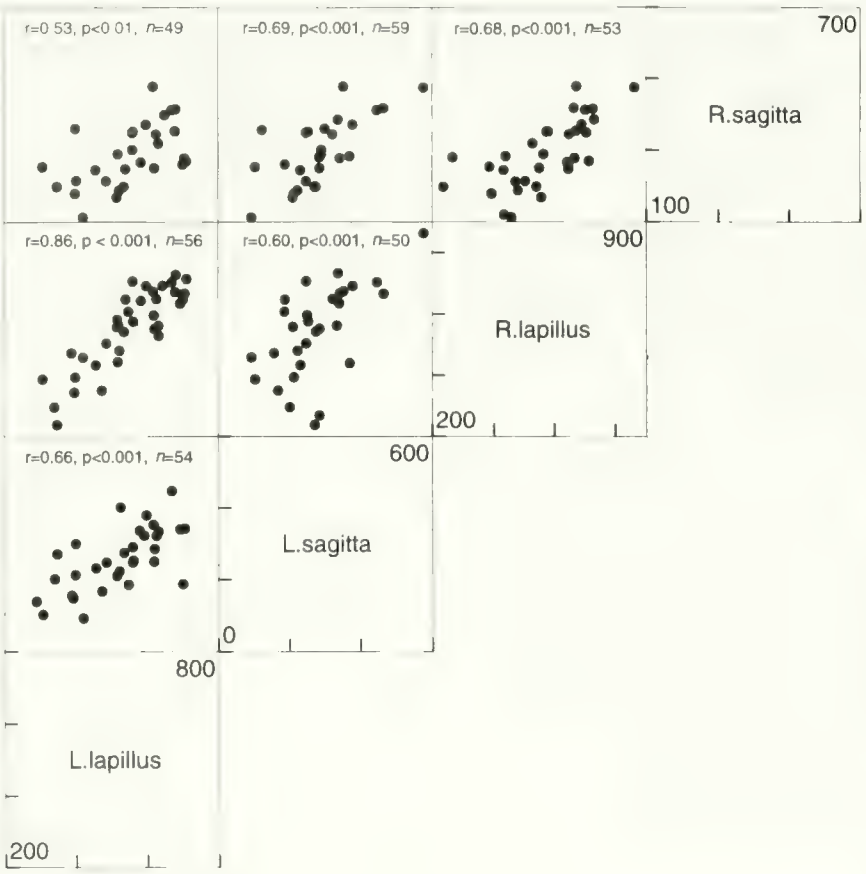

Figure 2

Scatter plots of individual measures of otolith area (μm^2) for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (r) for each relationship are given in each panel.

lapilli (Fig. 6). However, the residuals were not significantly related to either measure for sagittae.

Standard length (SL) at hatching was negatively related to sea temperature at collection: $SL = 5.26 (\pm 0.07) - 0.939(\pm 0.007) \times \text{temp}$, $n = 44$, $r^2 = 0.79$, $P = 0.001$. To explore the potential relationship between otolith size and temperature, we regressed our most predictive estimate of otolith size, lapillar area, against the residuals from the SL-temperature relationship. There was no clear relation between temperature residual and lapillar area (Fig. 7).

Discussion

Otoliths can be used to infer the standard length of cod larvae at hatching. However, our data suggest that the precision with which such inferences can be drawn may not be sufficient to permit accurate comparisons of the size distribution at hatching between survivors and the population at large. On the Scotian Shelf newly hatched cod larvae varied between 2.4 and 6.1 mm SL (Miller et al., 1995). The best regression relationship we developed in our study related SL to area of the lapillus, and explained 35% of the variation in the data. Accordingly, 65% of the variation remained unexplained. The regressions we developed suggest that the 95% confidence intervals of individual back-calculated size at hatching for a fish are wide. Predicted SL for larvae with average-size lapilli ranged from 3.66 to 5.41 mm. This covers fully 48.7% of the total range in initial sizes at hatching observed in cod larvae from the Scotian Shelf. More strikingly, based on estimates of mean and variation of SL given by Miller et al. (1995), this range includes 91% of all newly hatched cod larvae on the Scotian Shelf. Back calculations from lapillar otoliths larger or smaller than average size will be even more imprecise. Thus, we conclude that estimates of initial size in cod larvae are unlikely to be sufficiently pre-

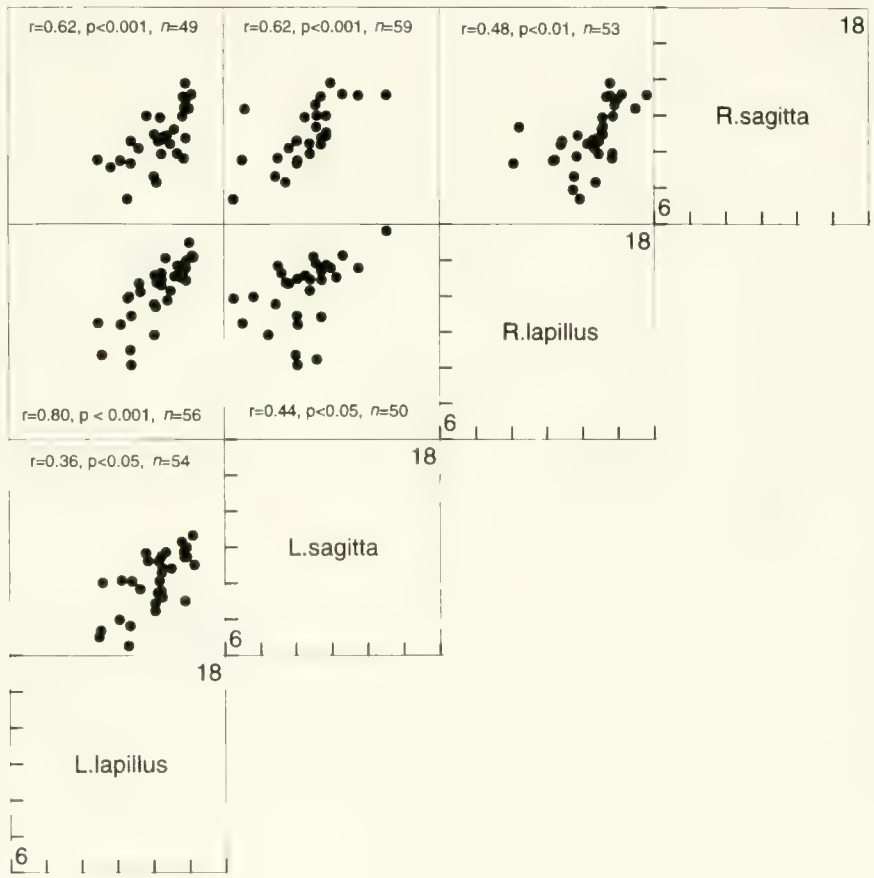

Figure 3

Scatter plots of individual measures of otolith diameter (mm) at hatching for newly hatched cod larvae collected on the Scotian Shelf. Correlation coefficients (r) and significance for each relationship are given in each panel.

cise to detect anything other than substantial differences in hatching size among the survivors and the initial cohort.

Meekan and Fortier (1996) reported evidence that surviving cod larvae on the Scotian Shelf in 1992–93 were significantly different from the cohort from which they originated. In contrast, survivors did not differ from the cohort at large in 1991–92. Meekan and Fortier (1996) suggested that the change in radius at hatching that they observed in 1992–93 was evidence of selection for faster growing larvae in that cohort. Meekan and Fortier's suggestion, as it relates to the relative sizes of otoliths in the survivors and the initial cohort, is indisputable. Our findings that the size of a larva and its otoliths are weakly correlated do not allow us to reject the notion that survivors may have differed in size at hatching from the overall cohort. Our results suggest an additional explanation. We report here a significant relationship between otolith size and the residual from the predicted relationship between egg and larval sizes. Larvae that hatch from relatively larger eggs, which have relatively larger yolks, have larger otoliths. Hence, we agree with the Meekan and Fortier's (1996) suggestion, but we would further hypothesize that the difference observed may have been caused by variation in egg size rather than by variation in larval size at hatching directly. If correct, we suggest that the greater amount of yolk in larger eggs enhanced initial larval growth and survival. An understanding of the actual mechanism responsible for these faster growing larvae will require additional analyses.

Our results suggest that attempts to backcalculate size of cod larvae will be most successful if they are based on measurements from the lapillus. Although larval SL at hatching was significantly related to all measures of otolith size, relationships involving the lapillus explained more variation than corresponding relationships involving the sagitta. Moreover, regressions involving the projected area of the lapil-

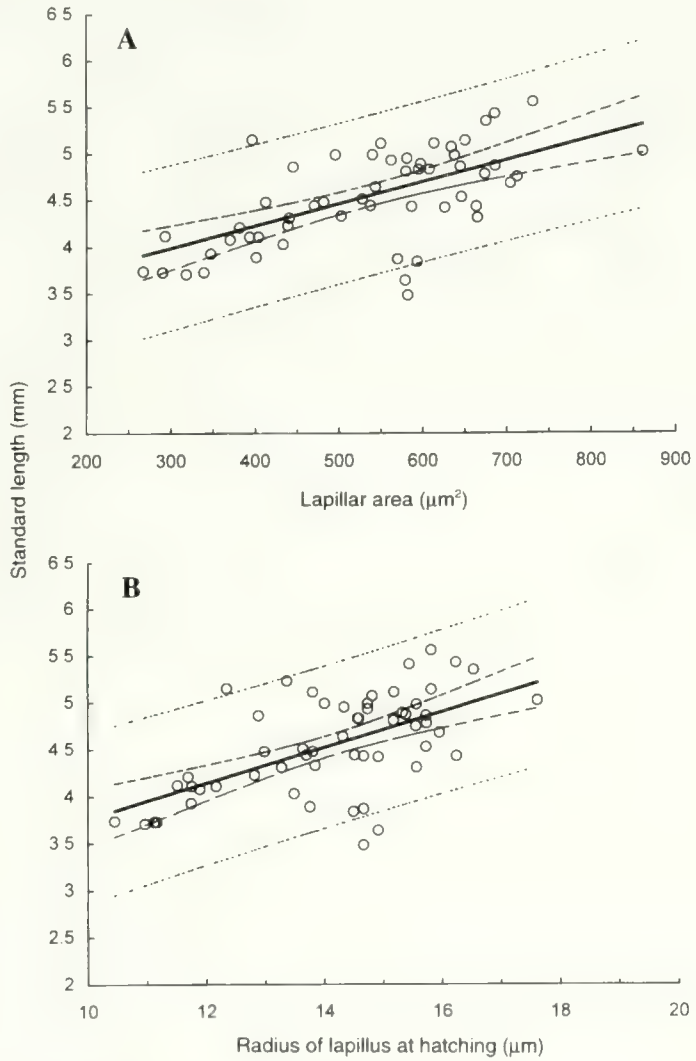

Figure 4

Relation between standard length (SL) at hatching of individual larvae and (**A**) the lapillar area (LA), and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $LA = 3.295\ (\pm 0.24) + 0.0023\ (\pm 0.0004) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$; $LR = 1.898\ (\pm 0.51) + 0.188\ (\pm 0.036) \times SL$, $n = 54$, $r^2 = 0.35$, $P = 0.0001$.

lus were more accurate than those involving the radius of the lapillus at hatching. We conclude from these findings that attempts to hindcast size at hatching in cod should rely on measurements taken from the lapillus and, where possible, should use the cross-sectional area of the otolith as the measure of otolith size. It has been recognized that cod lapilli are larger initially than sagittae, but that sagittae increase in size more rapidly (Bergstad, 1984; Radtke, 1984; Campana and Hurley, 1989). Lapilli remain larger than sagittae for up to 25 days. As a result, back calculations involving cod older than 25 d or larger than 6–8 mm have been based on sagittae instead of lapilli. However, the relative sizes of the otoliths at their core remain unaltered by subsequent growth dynamics. Hence, we caution that, even though the sagittae in these larger and older fish are larger absolutely than the lapilli, the precision of estimates of initial size at hatching will be most precise if the estimates are based on the size of the lapillus at hatching.

In controlled laboratory experiments, Geffen (1995) found that the otolith-size and fish-size relationship

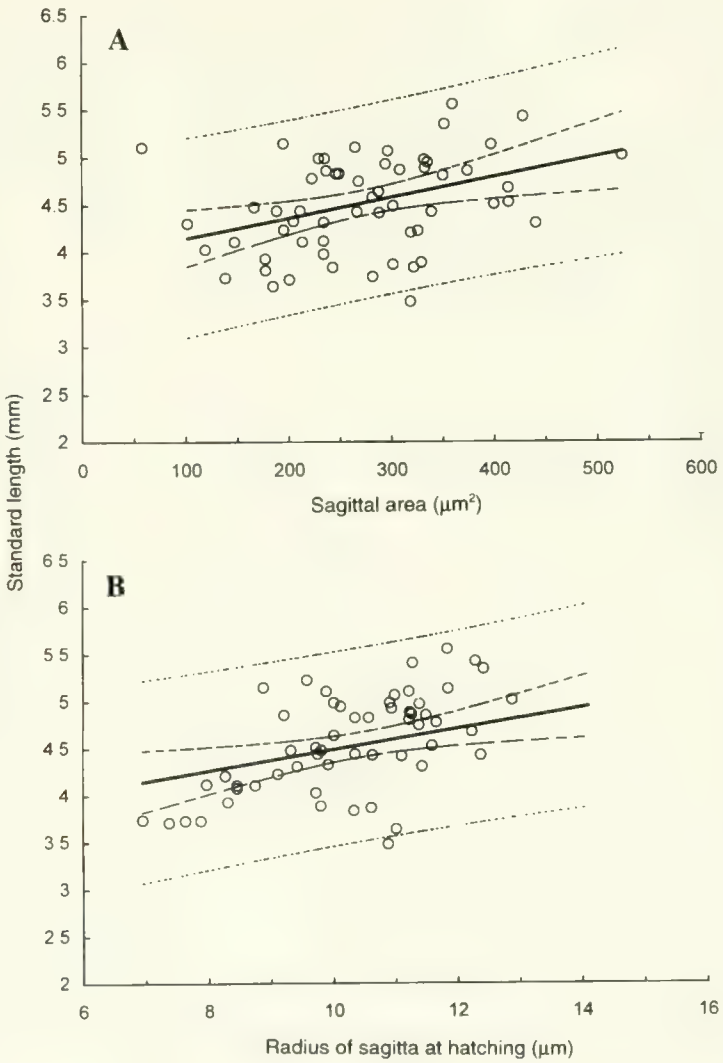

Figure 5

Relation between size at hatching of individual larvae and (**A**) the sagittal area (SA), and (**B**) the sagittal radius (SR) at hatching for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $SA = 4.033\ (\pm 0.21) + 0.00178\ (\pm 0.0007) \times SL$, $n = 58$, $r^2 = 0.09$, $P = 0.017$; $SR = 3.44\ (\pm 0.45) + 0.104\ (\pm 0.043) \times SL$, $n = 59$, $r^2 = 0.09$, $P = 0.018$.

could predict overall mean population growth rates extremely well but that they were unreliable predictors of individual larval growth. For example, Geffen (1995) reported that within 15 d of hatching, otolith growth and a measure of somatic growth were poorly correlated in cod larvae. If Geffen's conclusion reflects a broad pattern, her results have profound implications for any application of an individual-based backcalculation approach to cod. Recently, Meekan (1997) pointed out that Geffen's conclusions may have been affected by experimental conditions and by the use of a single mean value of larval size at hatching as the origin of the relationship between larval size and otolith size. Larval size at hatching varies substantially in cod (Knutsen and Tilseth, 1985; Miller et al., 1995), and thus Geffen's use of a single size at hatching is unrealistic and cannot be supported by the data available. Yet it is not clear what value one should use for the origin in backcalculating growth trajectories.

Our data suggest that the wide variability in the relationship between otolith size and hatching size observed in cod will likely plague attempts to

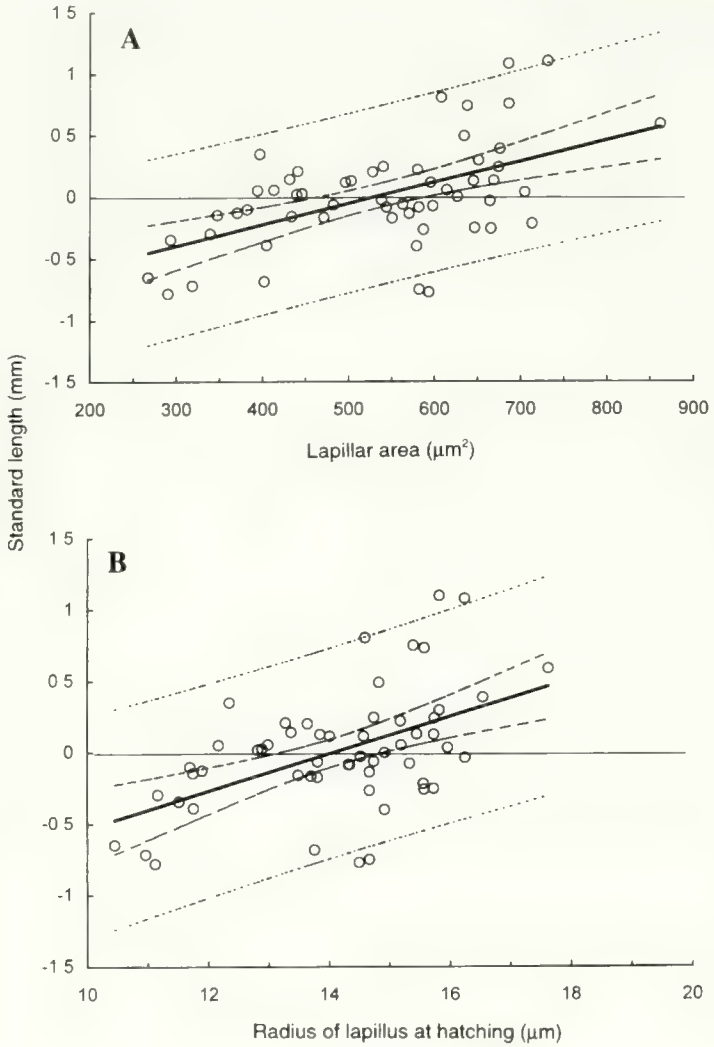

Figure 6

Relation between the residuals from the mean SL and mean egg diameter and **(A)** the lapillar area (LA) and **(B)** the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are: $Residual = 0.00162\ (\pm 0.0003) \times LA - 0.721\ (\pm 0.186)$, $n = 37$, $r^2 = 0.38$, $P = 0.0001$; $Residual = 0.126\ (\pm 0.03) \times LR - 1.633\ (\pm 0.39)$, $n = 37$, $r^2 = 0.37$, $P = 0.0001$.

backcalculate to early periods of the life history. Geffen (1995) commented on the variability in the sizes of hatchmarks on the lapilli of cod larvae. She reported estimates of otolith diameters at hatching that varied by more than twofold (13.7–28.4 μm). In Figure 8, we summarize published data on SL and lapillar diameter at hatching for a range of cod stocks. The variability evident in Figure 8 suggests that the choice of a "biological intercept" for cod is problematical (Campana, 1990); a single "best" size at hatching or otolith size at hatching clearly cannot be defined for cod. However, the data do show that an overall relationship between the mean SL at hatching and the mean diameter of lapillus exists. However, given the limited data set, the relationship is statistically insignificant ($MDL = 1.73 \times MSL + 19.54$, $r^2 = 0.306$, $n = 7$, $P > 0.05$). With these results, we recommend that extreme caution be exercised when selecting parameter estimates for use in the back calculation of size-at-age in cod.

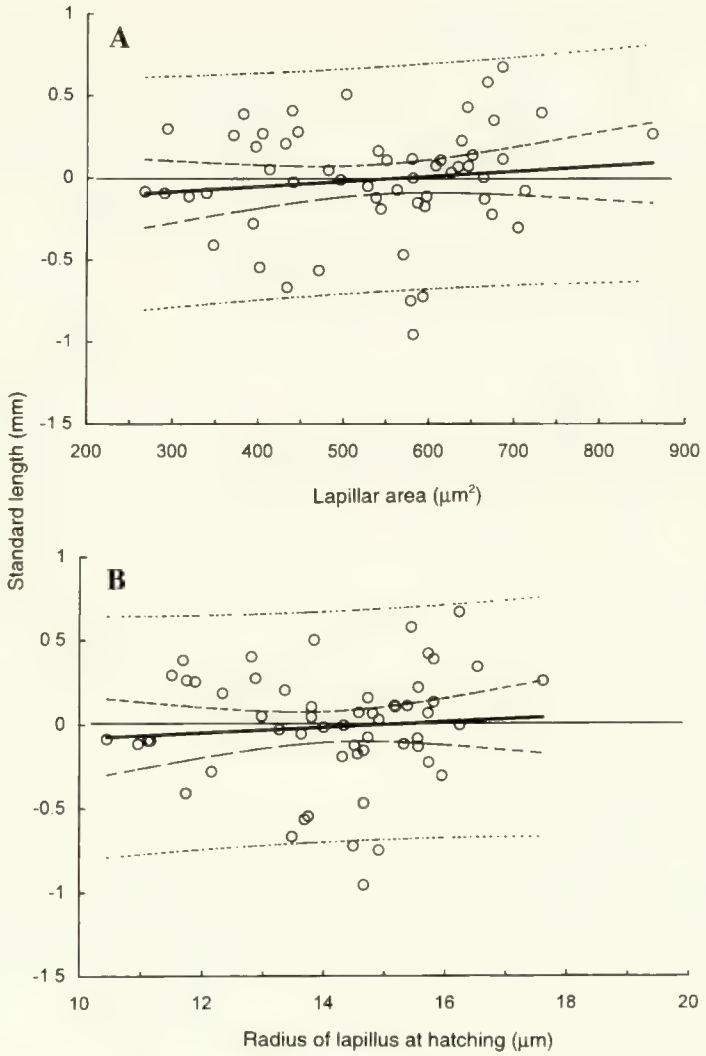

Figure 7

Relation between the residuals from mean SL and mean water temperature at collection and (**A**) the area of the lapillus (LA) and (**B**) the lapillar radius at hatching (LR) for newly hatched cod larvae on the Scotian Shelf. Shown on each plot are the predicted linear relationships and 95% confidence intervals of the mean and of individual predictions. Regression relationships are $Residual = 0.00021\ (\pm 0.00027) \times LA - 0.102\ (\pm\ 0.143)$, $n = 37$, $r^2 = 0.01$, $P = 0.89$; and $Residual = 0.013\ (\pm 0..21) \times LR - 0.184\ (\pm 0.28)$, $n = 37$, $r^2 = 0.001$, $P = 0.85$.

The implications from our results for studies on other species are less clear. It is important to note that one would not expect all species to exhibit the same plasticity in size at hatching, or in the relationship between fish size and otolith size at hatching. Hence, for some species there is little variation in initial size at hatching. In these species the error introduced by assuming a single, universal size at hatching is probably small. However, it is important to recognize that back-calculation techniques all assume a common origin for the family of size-at-age lines that are modeled. The methods differ only in the definition of the origin (fish size at zero otolith size, biological intercept, or otolith size at zero fish size), but all assume a single value. Indeed Campana (1990) noted that relatively little attention had been paid to the effects of variation in the intercept term of back-calculation methods; most attention had been paid to variation in the slope. However, for species that are known to vary widely in hatching size (e.g.

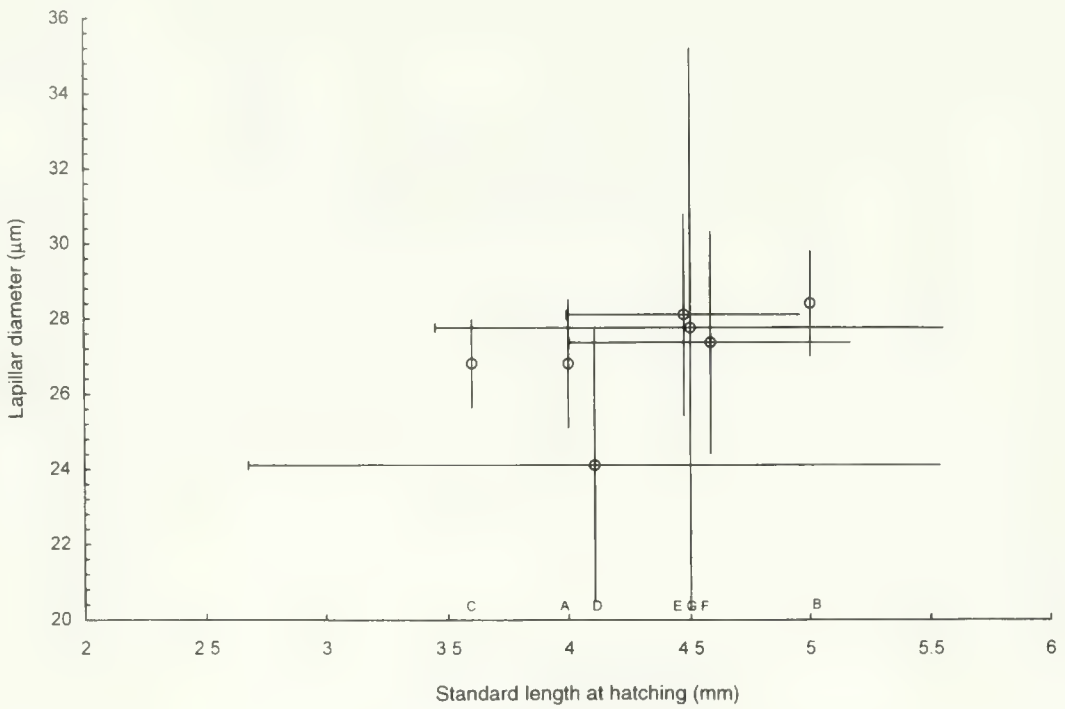

Figure 8

Relation between larval size and otolith size at hatching reported in the literature for different populations of cod. Shown for each data point are means and bivariate standard deviations (when available). The sources for individual data points are shown as letter codes above the abscissa. Codes: (**A**) Radtke (1984); (**B**) Bergstad (1984); (**C**) Radtke (1989); (**D**) Geffen (1995); (**E**) 1991–92 cohort from Meekan and Fortier (1996); (**F**) 1992–93 cohort from Meekan and Fortier (1996); and (**G**) this study. Estimates of SL at hatching for Meekan and Fortier were taken from estimates of mean hatching size for each cohort given by Miller et al. (1995).

Atlantic herring), individual variability in the intercept may be significant. We recommend that, at a minimum, stock specific values for intercepts be used if the interest is in periods of the life history shortly after hatching. Further, caution should be exercised in relating shifts in the back-calculated distribution of radii at hatching to size-selective mortality. More careful study of the relationship between otolith size and fish size in individual species is likely warranted if researchers wish to employ otolith-based back calculation (Chambers and Miller, 1995).

Acknowledgments

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Age validation and growth of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, on the Scotian Shelf

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Abstract.—Daily growth increments on otoliths were used to estimate the age of larval and juvenile haddock, *Melanogrammus aeglefinus*, and pollock, *Pollachius virens*, collected on Emerald and Sable Island Banks, eastern Canada, between March 1991 and May 1993. The daily periodicity of the increments was validated from observations of reared larvae. For both species, the first increment was deposited the day after hatching and thereafter one increment was added daily. A Laird-Gompertz growth curve was fitted to length–age data for each species. Growth rates in haddock and pollock larvae varied significantly in different years. For haddock, the lowest growth rate was for the 1993 cohort, and growth rates in 1991 and 1992 cohorts were similar. For pollock, the 1993 cohort had the highest growth rate. The average growth rate was 0.21 mm/d for the first month and 0.42 mm/d for the second month for larval haddock and 0.18 mm/d for the first month and 0.23 mm/d for the second month for larval pollock. Growth continued exponentially after the transition from a primarily pelagic life to a predominantly demersal one, which occurred at an age of about 40–50 d. No indication of a cessation in growth was observed. Analysis of length–age data indicated that the accelerated growth of juveniles after 50 d in age could have reflected the exploitation of a more abundant food resource after settlement. Thus, pelagic and early demersal growth appear to represent distinct stanzas in the growth history of these gadoids.

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A central problem in fisheries research is understanding mechanisms determining year-class strength. Growth, which is considered critical to the survival and subsequent recruitment of larval marine fishes (Houde, 1987), is likely strongly affected by temperature and food availability (Ricker, 1979). Food limitation can affect survival directly by causing starvation (Lasker, 1975) or indirectly by retarding growth rate which in turn increases mortality from predators (Rothschild and Rooth, 1982). In addition, feeding conditions may change markedly owing to density independent factors, such as temperature, which can directly affect growth rates (Laurence, 1978).

Ware (1975) suggested that growth and mortality rates interact to determine survival of fish populations. A prediction of this hypothesis is that predation is a major factor affecting year-class strength and that mortality due to predation is inversely related to growth rate (Ware, 1975; Shepherd and Cushing, 1980). This hypothesis assumes that average growth is below the maximum and that feeding conditions that maximize growth are associated with minimal mortality.

Calculation of reliable rates of growth and mortality of larval fish, and determination of when loss due to recruitment is greatest, requires accurate determinations of age. Accuracy and precision of growth estimates for larval fishes have been greatly enhanced by the discovery of daily growth increments on otoliths (Pannella, 1971; reviewed by Campana and Neilson, 1985). Ageing by counting otolith growth increments, along with measurements of the width of the increments, provides a means of estimating the relation between length at age. In this way, growth curves, and even individual growth rates, have been calculated for a variety of species (Brothers et al., 1976; Struhsaker and Uchiyama, 1976; Taubert and Coble, 1977; Radtke and Waiwood, 1980).

Daily increments have been shown to occur in most species, nevertheless validation of the frequency of increment deposition is required before larval age can be estimated from otolith measurements. To validate increment deposition, Geffen (1987) recommended sampling reared larvae throughout the larval stage. This approach had previously been used for a number of species, for example, to determine when the first increment is deposited in Atlantic cod (*Gadus morhua*) larvae (Radtke and Waiwood, 1980) and to validate the daily increment formation in Pacific herring (*Clupea pallasi*) (Moksness and Wespestad, 1989). In the present study, I vali-

dated whether increments are deposited daily in haddock otoliths (*Melanogrammus aeglefinus*) using the same approach. Preliminary results on larval pollock (*Pollachius virens*) are also presented. Finally, daily increment analyses are used to estimate age and growth rates of larval and juvenile haddock (*M. aeglefinus*) and pollock (*P. virens*) from the Emerald and Sable Island Banks on the Scotian Shelf off eastern Canada.

Materials and methods

Study area and collection of larvae

The Scotian Shelf is a 62,000 km^2 area with an average depth of 90 m. It is bounded on the southwest by Northeast Channel entering the Gulf of Maine and on the northeast by the Laurentian Channel and Gulf of St. Lawrence. Several shallow offshore banks along the outer edge of the shelf are separated from one another by deeper channels that open onto interior basins having depths of >100 m (O'Boyle et al., 1984). The general water circulation on the Scotian Shelf is dominated by the Scotian current which flows southwesterly and parallel to the Nova Scotia coast and which carries a mixture of slope water and diluted waters from the Gulf of St. Lawrence (e.g. Sutcliffe et al., 1976; Drinkwater et al., 1979).

Eggs, larvae, and juveniles of *M. aeglefinus* and *P. virens* were collected during 20 surveys made on Emerald and Sable Island Banks (Fig. 1) from March 1991 to May 1993 (Table 1), as part of the program of Ocean Production Enhancement Network (OPEN) (Griffin and Anderson, 1993). Sampling was conducted using a grid of 45 stations (Fig. 1) with an interstation spacing of approximately 30 km. A 50-cm bongo frame with 150- and 250-µm mesh nets (March–May 1991) as well as a rectangular midwater trawl (RMT, 2–8 m^2) (Baker et al., 1973) with nets of 2 m^2 (333-µm mesh) and 8 m^2 (1600-µm mesh) were used. At each station, duplicate oblique hauls were made from near the bottom to the surface at 2.0–2.5 knots, with a retrieval time of 30 min. After the standard grid stations were sampled, the area of maximum abundance of larval fish was revisited so that 48 h of vertical sampling could be conducted with a BIONESS sampler (1 m^2) (Eastern Marine Services E-Z-Net, Dartmouth, NS) fitted with ten 333-µm mesh nets (June 1991 to May 1993). Ten discrete depths were sampled every 4 h. Deployment sampling depths were spaced at 5-m intervals, from the bottom to the surface, and fished for 5 min at 2.0–2.5 knots. Most larval haddock and pollock were sorted at sea and preserved in 95% ethanol. Temperature and salinity profiles were recorded at each station

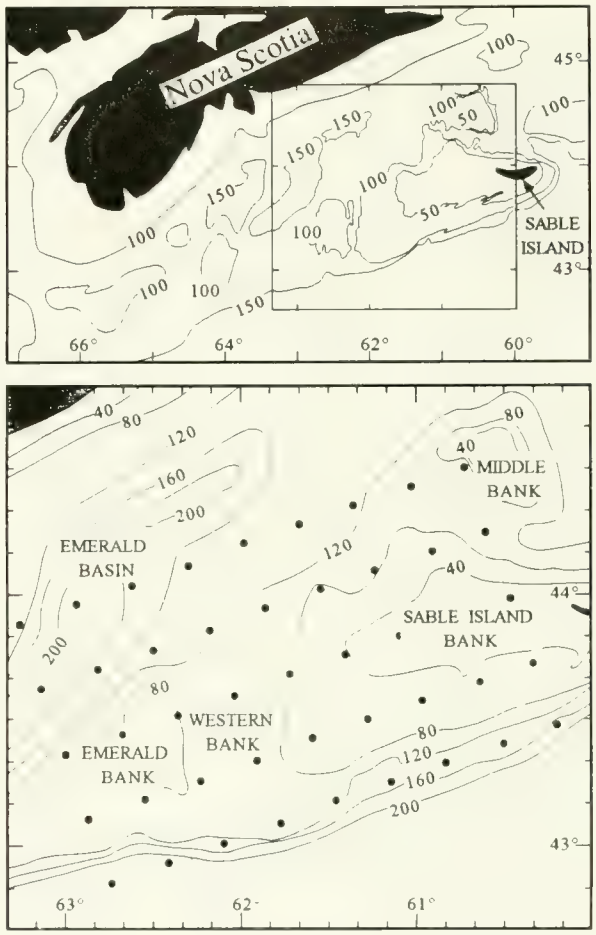

Figure 1

Study area showing stations where larval and juvenile haddock and pollock were collected on the Scotian Shelf from March 1991 to May 1993. Isobaths are in meters.

with a Sea Bird CTD probe (Sea-Bird Electronics, Inc. Bellevue, WA) connected to the electronics unit of the RMT or BIONESS sampler, or both. When the RMT or BIONESS, or both, were not used, independent CTD casts were made at each station.

A subset of pollock and haddock larvae were videotaped at sea by using a stereo dissecting microscope connected to a video camera and a magnetoscope and were then individually preserved in 95% ethanol. One to two months later, each fish was measured in the laboratory to the nearest 0.1 mm with a stereo dissecting microscope with an ocular micrometer. The unpreserved standard lengths were measured from video images recorded at sea and projected on a television monitor linked to an image analysis system. Linear regression of unpreserved standard length (SL, obtained from the videotape) to preserved standard length (*PSL*, after preservation in ethanol) for haddock (SL=1.531 + 1.005PSL, n=129, r^2=0.99) and pollock (SL=0.710 + 0.969PSL,

Table 1

Station information for larval and juvenile of haddock and pollock collected for otolith analysis from March 1991 to May 1993 on the Scotian Shelf. Values in parentheses are total larvae sampled.

Cruise	Vessel	Date	T (°C) at 30 m	No. of larvae examined		Mean SL of larvae (mm)		Mean no. of increments	
				Haddock	Pollock	Haddock	Pollock	Haddock	Pollock
91–01	*Petrel V*	5–11 Mar	4.0	0 (3)		3.9		—	
91–02	*Petrel V*	16–24 Apr	5.0	2 (97)		4.6		14	
91–04	*Petrel V*	17–26 May	7.0	1 (22)		7.6		23	
91–99	*Cape Keltic*	17–22 Jun	8.3	93 (164)		20.2		60	
91–08	*Petrel V*	18–27 Jul	13.5	18 (18)		60.8		105	
91–16	*Petrel V*	12–21 Nov	8.8		4 (16)		3.9		4
91–17	*Petrel V*	7–16 Dec	7.3		12 (23)		5.1		9
92–18	*Petrel V*	7–18 Jan	5.2		88 (98)		5.7		11
92–19	*Petrel V*	16–26 Feb	2.3	0 (9)	80 (218)	5.1	10.7		29
92–20	*Petrel V*	10–20 Mar	1.6	12 (66)	17 (61)	4.9	12	2	41
92–21	*Petrel V*	5–14 Apr	2.0	9 (40)	7 (33)	4.7	15	3	44
92–23	*Petrel V*	17–26 May	3.8	65 (328)	2(2)	8.1	22	21	70
92–98	*Cape Keltic*	17–22 Jun	7.3	16 (47)		22		60	
92–26	*Petrel V*	21–25 Jul	13.7	5 (5)		31.1		66	
93–32	*Petrel V*	11–22 Jan	4.0		246 (1005)		5.4		5
93–33	*Petrel V*	15–25 Feb	2.1		54 (57)		9.9		27
93–34	*Petrel V*	19–26 Mar	1.7	138 (266)	5 (5)	4.4	15.1	4	54
93–35	*Petrel V*	16–24 Apr	3.7	116 (239)	4 (4)	7.2	13.5	16	48
93–37	*Petrel V*	16–24 May	5.6	127 (290)	0 (10)	12.4	15.5	33	

n=8, r^2=0.99) were used to calculate the unpreserved standard length (SL) of fish preserved in ethanol.

Validation of ageing technique

To determine if the increments observed in otoliths of haddock and pollock were deposited daily, fertilized eggs collected in a 333 µm mesh net from the RMT were reared on the ship. Haddock eggs were collected at the Western and Emerald Banks area, February–April 1992 and 1993. Spawning begins in February around the Western Bank. Eggs were taken in the same general area on any given sampling date from February to April in both 1992 and 1993.

Some pollock eggs were collected in January–February and April 1992, as well as in October–November 1992 and January and March 1993. At the beginning of the spawning season, eggs were detected at the southeast of Sable Island Bank. In January–February the eggs were collected on the Western Bank, and in March–April the distribution of eggs included Emerald Bank. The spawning of pollock and haddock overlapped during February–April because the eggs of the two species were found together.

Immediately after the nets were brought aboard the vessel, the most advanced stages of eggs were sorted and individually placed in 20-mm vials filled with seawater which had been passed through 1-µm Hytrex filters. At this time it was impossible to distinguish between the eggs of the two species (Brander and Hurley, 1992). They were reared at 4°C in a conventional refrigerator on the ship. The photoperiod was kept at 12:12 h with dim blue light. As each egg was monitored twice daily to establish when hatching occurred, the maximum error in hatching time determinations was 12 h. After hatching, 136 zero to eleven-day haddock larvae, and nine zero to four-day pollock larvae were killed and preserved in 95% ethanol. Twelve additional 0–2 d old haddock larvae (collected on April 1993) were obtained from Flodevigen Marine Research Station, in Arendal, Norway. A total of 148 haddock larvae and 9 pollock larvae were used to examine increment formation. Because haddock and pollock eggs were indistinguishable; individuals were later identified by their larval characteristics.

Otolith preparation

A dissecting microscope illuminated with polarized light was used to dissect the sagittae and lapilli from larval skulls with the aid of fine needles. One thousand two hundred and sixty pairs of haddock and

pollock larval otoliths from the validation experiment and from wild fish <36 mm SL were mounted on glass over slides with Permount (Fisher Scientific Laboratory, Fair Lawn, NJ). Eighteen pairs of haddock otoliths from larvae measuring 50–83 mm SL were mounted with synthetic resin on metal stubs for SEM observation.

The mounted otoliths (sagittae) used in the validation experiment were read with an image analyzer system by using Optimas software (Subtechnique, Inc., Alexandria, VA). Otoliths from field-collected larvae and juveniles were read at the Southwest Fisheries Center (La Jolla, CA) by using the OTO program (Andersen and Mokness, 1988). The image analyzer system consisted of a video camera attached to a compound microscope, monitor, digitizer, and microcomputer. A detailed description of the OTO program, otolith analyzing system, and methods used are given by Andersen and Moksness (1988). Otoliths examined with SEM were ground on the sagittal plane to the nucleus with fine grit paper (between 30 µm and 0.3 µm), and then the polished surface was etched for 6 min in 0.2M EDTA (pH 7.6).

In addition to the number of increments, the following otolith measurements were taken and used in comparisons of each species: maximum otolith diameter (OD); maximum otolith radius from the center of the nucleus to the outer edge of the otolith (OR); diameter of the otolith nucleus (ON); and diameter of the yolksac resorption check (YSC) as defined by Radtke and Waiwood (1980) and Bolz and Lough (1983). Growth increments were counted twice by the same reader at an interval of 3 mo between readings. The two counts usually differed <6%, and the average was used as an estimate of age.

Statistical procedures

For both species, of all otolith measurements, the maximum otolith diameter was most strongly correlated with length. I compared the relation of otolith growth to larval growth between month and year for both species to determine whether otolith growth could be used to predict larval growth. Thus, linear regressions of LnSL on LnOD were compared by using analysis of covariance (ANCOVA) with OD as the covariate.

A Laird-Gompertz growth model curve was fitted to the length-at-age data for each species in each year. This model has been shown to provide an adequate fit for length-at-age data on age 0+ fish of many different species (Bolz and Lough, 1988; Lough et al., 1982; Watanabe et al., 1988; Simard et al., 1992). Zweifel and Lasker (1976) presented a detailed discussion of the Laird-Gompertz function. The equation for the model is

$$L_t = L_0 e^{k(1-e^{-at})},$$

where L_0 = length at t=0;
k = a dimensionless parameter, such that ka=A_0 is the specific growth rate at t=0 (A_t=$A_0 e^{-at}$);
L_t = length at any age t;
a = the specific rate of growth when t=t_0; and
t_0 = the time when the growth rate starts to decrease, that is, the inflection point of the curve (Ricker, 1979).

The parameters were derived by nonlinear least squares tests by using the SYSTAT nonlinear program (Wilkinson, 1990), and ANCOVA was used to test whether differences in growth rates in different years of each species were significant.

Results

Validation of daily increment deposition

In both species, otoliths (sagittae and lapilli) were present at hatching. Some haddock otoliths (Fig. 2A) showed one to three irregular increments between the nucleus and the check at hatching, as observed by Bolz and Lough (1983). The mean (±SD) diameters of the nucleus and of the check at hatching of reared larvae were 10.8 ±2.5 and 21.4 ±3.3 µm, respectively, in haddock and 12.0 ±1.9 and 20.7 ±2.2 µm, respectively, in pollock. The values for haddock were consistent with earlier reports by Bolz and Lough (1983) and Campana (1989). In both species, increments appeared as alternate light and dark zones (Fig. 2), and the first regular increment was formed the day after hatching (Table 2). The number of increments (NI) corresponded to the chronological age in d (AGE) of the larvae (Fig. 3). The slopes of the regressions for haddock (NI=0.99 AGE, n=148, r^2=0.96, P>0.0001) and pollock (NI=1.09 AGE, n=9, r^2=0.82, P=0.0005) did not differ significantly from 1 (t-test, P=0.637 for haddock and P=0.890 for pollock).

Growth of haddock and pollock otoliths

The check at hatching was clearly visible and increments were easily distinguished in the otoliths of larvae sampled at sea (Fig. 4). The nuclear and check diameters at hatching for haddock and pollock differed in different years (ANOVA, P<0.01) (Table 3). For haddock, differences in nuclear check diameters between 1991 and 1993 were not significant (ANOVA, P>0.05). There were no significant differences among

years for yolksac check diameters for either haddock or pollock larvae (ANOVA, $P>0.05$). Within some haddock otolith nuclei, 1–3 increments were observed. Outside the nucleus, 6–8 growth increments of irregular width were observed between the nucleus check and a second well-marked check. Bolz and Lough (1983) observed 2–8 faint increments bounded by a discontinuous zone that appeared to be analogous to the yolksac check found in larval cod otoliths by Radtke and Waiwood (1980). Accordingly, I interpreted the second well-defined mark as a check resulting from yolksac resorption. The mean diameter of the yolksac check was 34.9 ±2.8 µm in haddock and 35.3 ±2.6 µm in pollock. Several (mean 7 ± 1.8) narrow (<1 µm) increments were found immediately after the yolksac resorption check. Increment width increased rapidly in subsequent increments.

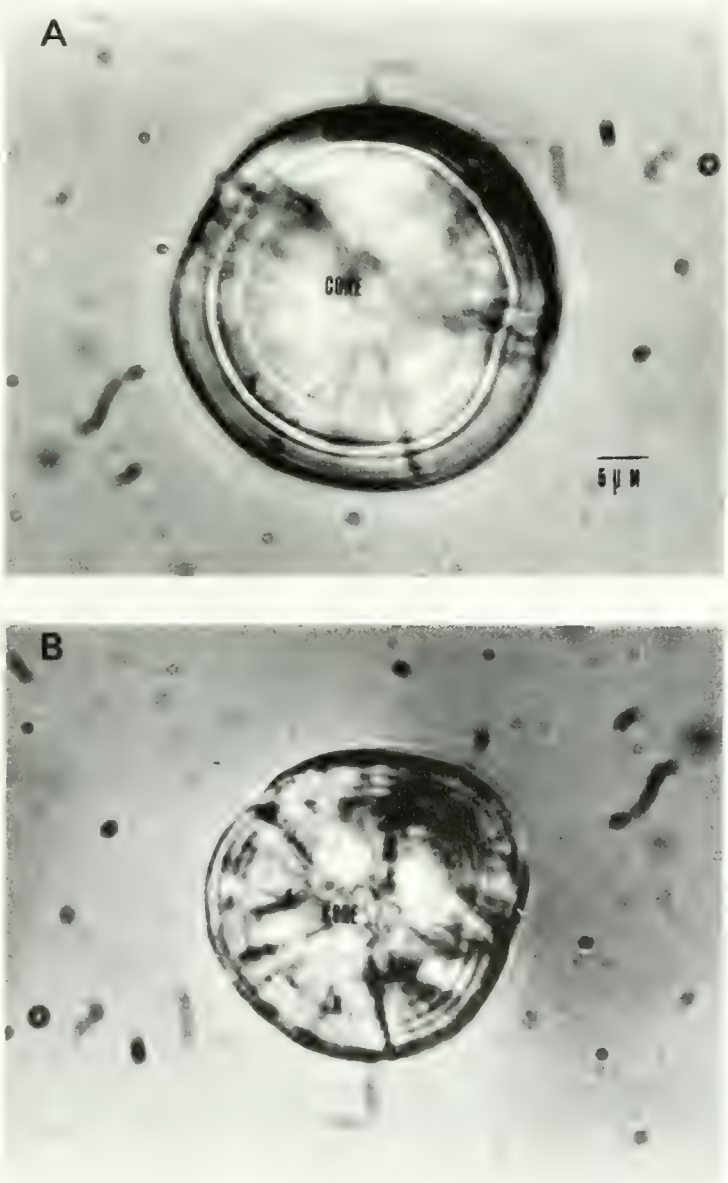

Figure 2

Light micrographs of sagittae. (**A**) Sagitta from a 5.93-mm, 5-day-old, haddock larva. (**B**) Saggita from a 4.98-mm, 3-day-old, pollock larva. H = hatch check. Growth increments appear as light and dark zones. The larvae were hatched from eggs collected from the Western and Emerald Banks area. Bar represents 5 µm.

The relation between otolith and larval fish sizes was best described by a ln-ln regression (Fig. 5). For haddock and pollock, significant differences were found between cruises (ANCOVA, $P<0.05$); however, no significant differences were found among years (ANCOVA, $P>0.05$) for either species (Table 4). Among haddock samples, a multiple range test revealed four homogeneous groupings in the samples from the ten cruises analyzed ($P<0.01$). The groupings were interpretable in terms of monthly sagittal growth. The first group integrated larvae from March to April; the second, larvae from May; the third, larvae from June; and the fourth, larvae from July. With pollock, the multiple range test showed three homogeneous groupings among the pollock sampled during the ten cruises ($P<0.01$). The first group integrated larvae from November to January; the second, larvae from February; and the third, larvae from March to April. It was possible to distinguish different stages in sagittal growth from otolith structure. Sagittae from the early developmental stages of haddock and pollock larvae were almost circular in shape, and there was one flat and one convex-side, accessory nucleus developed in the sagittae of postlarvae. As the larvae developed, the otoliths grew faster along the anteroposterior axis and became oval shaped.

Haddock and pollock larval and juvenile growth

For both haddock and pollock, the first otolith increment was laid down the day after hatching. Thus, the age of larvae and juveniles was indicated by the number of increments in the sagittae. Daily increments were counted in otoliths from 1121 individuals of a total of 3126 cap-

Table 2

Chronological age (from hatching), otolith diameter, and increment formation in reared larval haddock and pollock.

Chronological age (days)	Standard length (mm)	Otolith diameter (μm)	Increment	± SD	Number of larvae
Haddock					
0	4.69	26.70	0.5	0.5	18
1	4.75	27.87	1.1	0.2	15
2	5.12	30.04	2.1	0.3	21
3	5.16	32.11	3	0.4	15
4	5.68	33.03	4.1	0.4	26
5	5.74	34.03	5.1	0.3	13
6	5.86	34.04	5.8	0.6	23
7	5.90	34.41	6.6	0.8	9
8	5.86	36.45	7.3	0.4	4
9	5.77	36.92	8.5	0.5	2
10	5.84	37.58	10	—	1
11	6.19	37.67	11	—	1
Pollock					
0	4.10	24.72	1	—	1
1	3.81	26.10	1	—	1
2	4.34	29.38	2	0	3
3	5.00	28.78	3.3	0.5	3
4	4.49	32.49	4	—	1

tured. Haddock larvae and juveniles (n=602) ranged from 2.7 to 83.0 mm in SL and from 0 to 128 d in age, and pollock larvae and juveniles (n=519) from 2.8 to 23.8 mm in SL and from 0 to 84 d in age. For each year, Gompertz growth curves were fitted to describe the mean growth of larval and juvenile haddock (1991, 1992, and 1993) and pollock (1992 and 1993) (Fig. 6; Table 5). Length at hatching predicted from the curves was 4.1 mm for haddock and 4.5 mm for pollock, both within the range reported by previous studies (Fridgeirsson, 1978; Bolz and Lough, 1983; Fahay, 1983). Because the predicted inflection point for both haddock and pollock curves fell beyond the length range analyzed, the end of the first growing season had not been reached.

Although haddock larvae older than 80 d were obtained in 1991 and 1992, they were not used in the comparison of growth. Haddock growth rates (mm/d) during the first 80-d period in 1993 were different from those in 1991, and growth rates in 1993 were different from those in 1992 (ANCOVA, P<0.01) (Table 6). The 1993 cohort had the lowest growth rate. The 1991 and 1992 cohorts had similar growth rates (ANCOVA, P=0.84). The average growth rate of larvae was 0.21 mm/d during the first month and 0.42 mm/d during the second month. Growth continued exponentially from the predicted length at hatching throughout the size range of larvae and juvenile collected, there being no indication of a cessation in growth.

Pollock growth rates (mm/d) varied significantly among years (ANCOVA, P<0.01) (Table 6). However,

Table 3

ANOVA of nucleus, hatching, and yolksac checks on year for haddock and pollock larvae collected on the Scotian Shelf.

		1991	1992	1993	F	$P>F$
Haddock	Nucleus[1]	15.7	16.9	15.5	40.8	0.00
	SD	1.4	1.3	1.4		
	Hatching	22.4	25.1	23.5	34.9	0.00
	SD	2.6	3	2.1		
	Yolksac	36.6	38.7	35	0.28	0.76
	SD	3.9	4.1	2.7		
Pollock	Nucleus		14.8	15.9	38.7	0.00
	SD		1.6	1.8		
	Hatching		23.9	23.1	38.1	0.00
	SD		1.4	1.9		
	Yolksac		35.6	35.1	5.2	0.02
	SD		2.6	2.7		

[1] Nucleus check 1991 versus 1993 not significant (P>0.42)

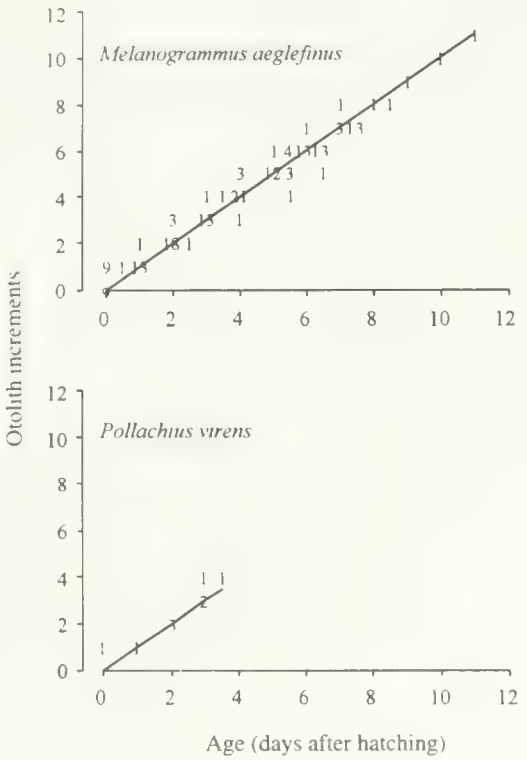

Figure 3

Number of increments enumerated on the sagittae of haddock and pollock larvae as a function of known age (days after hatching). Numbers represent the number of larvae. The number of increments (NI) corresponds to the chronological age in d (AGE) of the larvae. Haddock $NI = 0.99\ AGE$, $n = 148$, $r^2 = 0.96$, and pollock $NI = 1.09\ AGE$, $n = 9$, $r^2 = 0.82$.

the A_0 (specific growth rate at t=0) did not vary significantly (ANCOVA, P>0.05). The 1992 cohort had the higher growth rates during the first 50 d following hatching. Growth was linear at 0.18 mm/d following the predicted hatching size (1992 cohort), 0.13 mm/d (1993 cohort) through the first month, and 0.23 (1992 cohort) and 0.24 mm/d (1993 cohort) through the second month.

Discussion and conclusions

Validation of increment deposition

The present study shows that growth increments in haddock otoliths are formed daily and suggests that this is also the case in pollock. In both species, the first of the regular increments is formed on the day after hatching, and thereafter an additional increment is added each day up to 11 d for haddock and 4 d for pollock. Otoliths develop before hatching, and in haddock, 1 to 3 irregular increments are deposited prior to hatching. These types of irregular increments were not observed on larval otoliths of pollock. A few embryonic growth increments of a lamellar structure (such as I observed in haddock), have also been reported in other species (Brothers et al., 1976; Radtke and Dean, 1982; Watanabe et al., 1982; Nishimura and Yamada, 1984; Palomera et al., 1988). The spacing of embryonic increments is irregular, in contrast to regularly spaced posthatching increments, which indicates that they might not be deposited at daily intervals. Whereas Radtke and Waiwood (1980) did not observe increments formed prior to hatching in cod (*G. morhua*), they did observe regular increments that were formed daily starting one day after hatching. Brothers and McFarland (1981) noted three diffuse increments in the otolith core of French grunt (*Haemulon flavolineatum*) and speculated that they were deposited during the embryonic stage. Bolz and Lough (1983) found 1–2 poorly defined increments enclosed by the nuclear check in haddock larvae. According to the above observations, it seems reasonable to infer that the 1–3 irregular increments inside the hatch check of haddock otoliths are formed sometime during the 2–3 week egg stage (Laurence and Rogers, 1976; Fridgeirsson, 1978).

Growth of haddock and pollock otoliths

The sagittal otoliths of haddock and pollock larvae are circular in shape at the age of 35–40 d. Subsequent sagittal growth is greater along the anteroposterior plane, so that the otoliths become oval shaped in older larvae. Radtke (1989) reported that cod (*G. morhua*) sagittae change as they grow, from spherical to elongated to crenulated over a 65-d period. In haddock and pollock larvae, circular-shaped sagittae were observed until 8 mm SL, corresponding to an age of 35–40 d. Then, the sagittal shape begins to elongate as the result of growth of peripheral primordia, which corresponds to 30 mm SL (75–80 d) in haddock and 23 mm SL (80 d) in pollock. Thereafter the sagittae are not easily broken, and their shape is distinguishable from that of other gadoid species. The last changes in otolith shape correspond to the age when juveniles undergo metamorphosis to begin demersal life. Koeller et al. (1986) inferred, from a series of midwater and botton trawl surveys conducted in 1983 off southwestern Nova Scotia, that the transition to the demersal habitat by haddock occurs from June to August.

In most otoliths examined, I observed a well-defined, dark and discontinuous zone or ring laid down

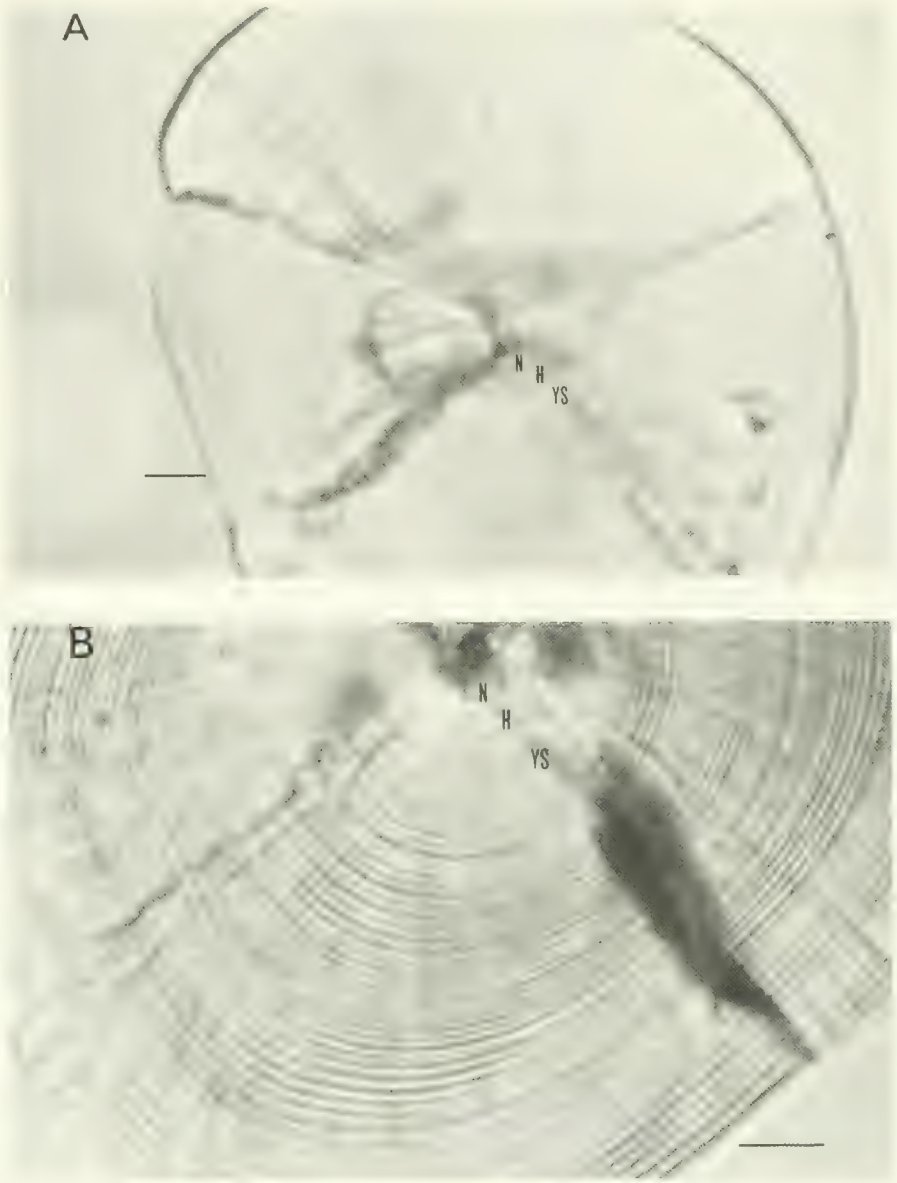

Figure 4

Light micrographs of sagittae showing different landmark checks. (**A**) Sagitta from a 13.7-mm-SL, 37-day-old haddock. (**B**) Sagitta from a 12.4-mm-SL, 50-day-old pollock. N = nuclear check, H = check at hatching, and YS = yolksac check. Bar of photograph represents 10 μm.

around the nucleus. It was the first mark presented in larval otoliths (Bolz and Lough, 1983; Radtke and Waiwood, 1980; Campana, 1989). Outside the nucleus, four to eight irregularly spaced increments were bounded by a discontinuous zone which appeared to be the yolksac check (Bolz and Lough, 1983). Laurence (1974) reported that at 7°C yolksac exhaustion occurs 6–7 d after hatching for haddock, and Fridgeirsson (1978) observed that at 7.2°C yolksac exhaustion occurs within 6 d for haddock larvae and 8 d for pollock larvae. From the regression of larval length to sagittal diameter, I estimated that yolksac resorption occurs at a standard length of 5.0 mm in haddock (at 3.5°C) and 5.1 mm in pollock larvae (at 5.0°C), corresponding to a mean age of 9 and 5 d, respectively. Fridgeirsson (1978) reported that haddock start independent feeding at 6–10 d after hatching and pollock at 8–10 d after hatching.

This suggests that the observed check is deposited at or immediately before yolksac absorption and that the number of increments between the nucleus and the absorption check reflects the duration of the yolksac phase (Fridgeirsson, 1978; Laurence, 1978; Fahay, 1983).

Haddock and pollock larval and juvenile growth

In recent years, the examination of otolith microstructure has resulted in many applications (Jones, 1992). The underlying assumption is that increments form daily. In otoliths of haddock (*M. aeglefinus*), and pollock (*P. virens*), increments are deposited daily and thus can provide accurate estimates of age (Bolz and Lough, 1983; Campana, 1989; Campana and Hurley, 1989).

The estimates of haddock growth in this study are comparable with those reported earlier. Thus, the predicted length of 4.1 mm at hatching and the average growth rate of 0.65 mm/d for 0–4 mo old larvae in the present study are similar to the values reported by Bolz and Lough (1983, 1988). The adjustment of a Laird-Gompertz model (r^2=0.99) for the entire data set correctly predicted length (Table 5). Different patterns in growth occur during ontogeny (Table 6). The average increase in length is moderate between hatching and 50 d (0.27 mm/d), high for early juveniles of 2.5–3 mo (0.68 mm/d), and moderate again (1.2 mm/d) for older juvenile. Few studies provide estimates of the age and growth of larval and juvenile pollock (Campana, 1989). The predicted length at hatching was 4.5 mm and the average growth rate of larval was 0.22 mm/d during the first 3 mo. The Laird-Gompertz model (r^2=0.98) applied to the entire set data adequately described growth. A slow increase in length occurs during the first 30 d after hatching (0.18 mm/d), and then the rate is moderate during the following 1 to 2 mo (0.23 mm/d). Finally, a stable period (0.24 mm/d) begins (Table 6). In the present study only the pelagic phase prior to metamorphosis and beginning of demersal life was examined. Nevertheless, sampling continued throughout the year and older pollock juveniles up to 80 d old (23 mm SL) were captured. The last pollock samples were collected in 1993. Juvenile pollock probably move from the oceanic zone to the shallow coastal zone after metamorphosis (Scott and Scott, 1988). Campana (1989) collected 53 pollock juveniles from the north shore of Gran Manan Island, New Brunswick, on August 1984, and the mean length of juveniles was 97.3 ± 1.9 mm. The date of capture of Campana's samples suggest that pollock juvenile move to the Scotian shore, possibly toward the Bay of Fundy, to finish their development. If pollock sharply increase their growth rate in response to improved feeding conditions during demersal lifestyle, as we observed for haddock, they could attain an average length of 106 mm by August, a size similar to that of juveniles collected by Campana. Growth rates (mm/d) varied significantly in different years, and the rates of the two cohorts showed an alternate pattern: growth was higher for the 1992 cohort during the first 45 d and higher for 1993 cohort following the first 45 d. The 1993 cohort was first detected two months later than the 1992 cohort. The adjustment of a Laird-Gompertz model (r^2=0.98) to each annual data set closely predicted length (Table 5).

Growth during the juvenile period of haddock and pollock can be divided into a series of "stanzas." The change from one stanza to the next is characterized by a discontinuity in development, such as during hatching or after a change of habitat (Ricker, 1979). Growth accelerates abruptly in fish older than 50 d in response to a shift from a pelagic to a demersal diet. Because we captured juvenile pollock immediately after the transition

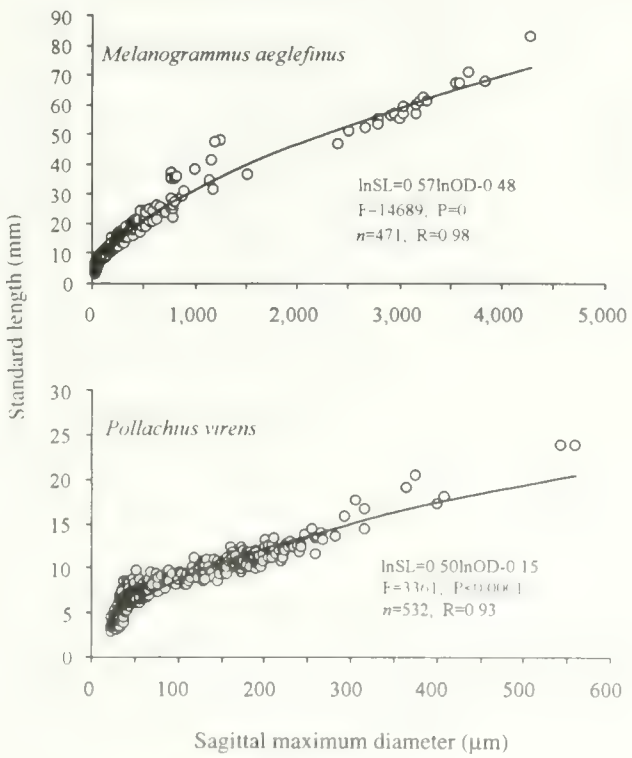

Figure 5

Standard length as a function of maximum sagittal diameter in larval pollock and haddock.

Table 4

Parameter estimates of the relationship between standard length and sagittal diameter for larval haddock and pollock collected on the Scotian Shelf. $\mathrm{Ln}SL = a + b\mathrm{LnSD}$. Note: The reduced correlation during March 1992 and 1993 for larval haddock is the result of differences between size of larvae and sagittal diameter at hatching.

			Intercept (a)		Slope (b)			
Species	Year	Month	Estimate	SE	Estimate	SE	n	r^2
Haddock	1991	June	0.006	0.090	0.477	0.014	37	0.97
		July	−3.140	0.442	0.898	0.055	18	0.94
	1991		−0.524	0.077	0.567	0.011	55	0.98
	1992	March	0.840	0.781	0.157	0.216	12	0.05
		April	−0.998	0.422	0.705	0.120	12	0.77
		May	0.068	0.101	0.466	0.022	65	0.87
		June	−0.002	0.167	0.500	0.027	16	0.96
		July	−0.722	0.530	0.594	0.078	5	0.95
	1992		−0.466	0.059	0.572	0.012	110	0.95
	1993	March	−4.574	0.467	1.733	0.134	134	0.56
		April	−0.618	0.162	0.612	0.038	45	0.86
		May	0.047	0.056	0.466	0.011	127	0.94
	1993		−0.469	0.032	0.564	0.007	306	0.95
		All	−0.445	0.021	0.560	0.004	471	0.97
Pollock	1991	November	2.162	0.239	−0.224	0.069	4	0.84
		December	−0.646	0.409	0.613	0.113	12	0.75
	1992	January	−0.943	0.154	0.717	0.041	91	0.77
		February	−0.095	0.093	0.482	0.019	80	0.89
		March	−1.011	0.325	0.644	0.060	17	0.88
		April	−0.463	0.469	0.568	0.087	7	0.90
	1991–1992		−0.143	0.045	0.494	0.010	211	0.92
	1993	January	−0.932	0.132	0.720	0.036	258	0.60
		February	0.694	0.119	0.326	0.024	54	0.78
		March	−0.856	0.334	0.632	0.060	5	0.97
		April	−0.392	0.505	0.538	0.091	4	0.95
	1993		−0.204	0.057	0.517	0.015	321	0.80
		All	−0.143	0.036	0.498	0.009	532	0.86

to a demersal life stage, it was possible that individuals were present in both pelagic and demersal zones at this time. Perhaps pollock juveniles were moving from the oceanic to the coastal zone; if so, this change in habitat could explain the reduction in numbers of juvenile older than 60 d in our sampling. I assume that conclusions drawn for juvenile haddock are valid only during the first eighty days for pollock. This period corresponds to the transition from a primarily pelagic to predominantly demersal life stage, which occurs when haddock reach about 20–25 mm in length (Koeller et al., 1986) and when pollock reach 10–15 mm. Although >25-mm haddock were captured in the water column, they probably had adopted a predominantly demersal life style. Thus, the acceleration in growth of >50-d juveniles could have reflected exploitation of abundant food resource after settling on the bottom (Mahon and Neilson, 1987).

In the present study, average growth rates were 0.21 mm/d in the first month and 0.42 mm/d in the second month for larval haddock and 0.18 mm/d in the first month and 0.23 mm/d in the second month for larval pollock. Growth continued exponentially

Table 5

Estimates of Gompertz model parameters for larval and juvenile haddock and pollock collected on the Scotian Shelf. L_0 = lenght at age $t = 0$, a = specific rate of growth at $t = t_0$, and k=dimensionless parameter.

Species	Year	L_0	a	k	n	r^2
Haddock	1991	2.478	0.010	4.954	114	0.99
	1992	3.609	0.006	6.172	107	0.99
	1993	4.317	0.005	5.809	381	0.99
	All	4.198	0.005	6.581	602	0.99
Pollock	1991–92	4.213	0.013	2.483	210	0.99
	1993	4.617	0.017	1.970	309	0.98
	All	4.569	0.013	2.429	519	0.98

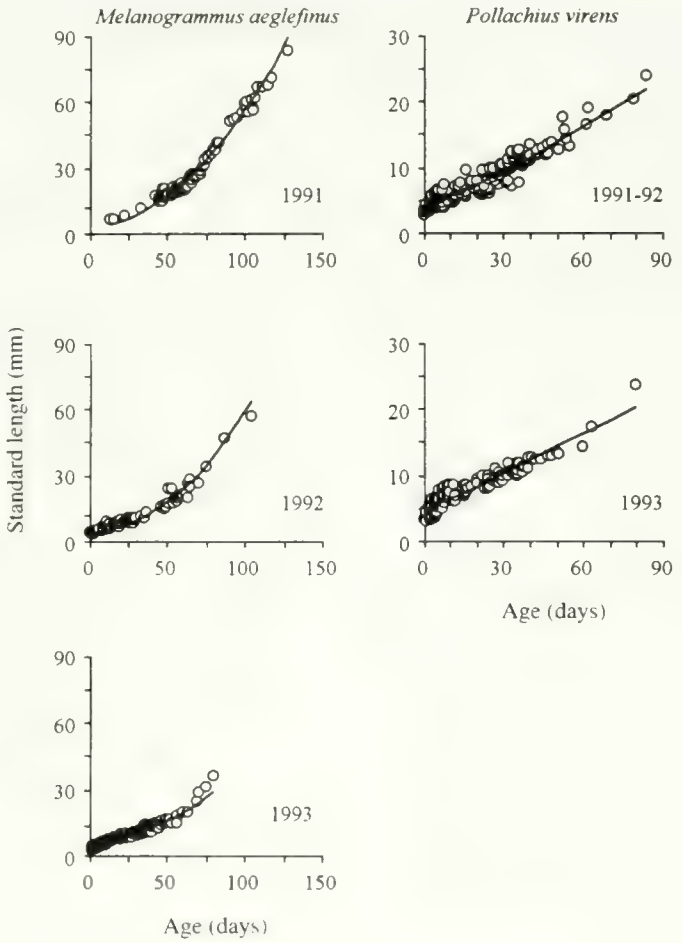

Figure 6

Estimated age versus length for larval and juvenile pollock and haddock. Lines were fitted by using the Laird-Gompertz growth model. Parameters of the model are shown in Table 5.

from the predicted length at hatching throughout the size range of larvae and juvenile collected. Otolith growth increments are suitable for estimating age, and the analysis of length–age data for young haddock and pollock on Emerald and Sable Island Banks suggests that the growth rate increases sharply at the transition from a pelagic to demersal life stage. Thus, pelagic and early demersal growth likely represents distinct "stanzas" in the growth history of these gadoids, and these "stanzas" may have different effects on recruitment variability. Rapid juvenile growth may increase juvenile survivorship by decreasing the time during which juvenile are exposed to predators (Houde, 1987). Interannual variation in juvenile growth rates may influence interannual variation in juvenile survivorship. Additional complicating factors during the pelagic phase of juvenile fish, such as different residence times and diel migrations in the water column (Koeller et al., 1986), reduce the possibility of identifing correlations between interannual variation in growth rates and environmental factors, and thereby allow predictions of recruitment success.

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Table 6

Growth rate (mm/d and %/d) of larval and juvenile haddock and pollock estimated from the Laird-Gompertz growth model.

	Haddock								Pollock					
	Growth rates (mm/d)				Growth rates (%/d)				Growth rates (mm/d)			Growth rates (%/d)		
Age (days)	1991	1992	1993	All	1991	1992	1993	All	1992	1993	All	1992	1993	All
0	0.13	0.13	0.11	0.14	4.00	3.70	2.56	3.85	0.14	0.10	0.14	3.23	1.85	3.16
5	0.16	0.16	0.12	0.16	3.86	3.59	2.56	3.72	0.15	0.10	0.16	3.02	1.85	2.96
10	0.18	0.18	0.14	0.18	3.73	3.49	2.56	3.59	0.16	0.11	0.17	2.83	1.85	2.77
15	0.21	0.21	0.16	0.21	3.60	3.38	2.56	3.47	0.17	0.13	0.18	2.66	1.84	2.60
20	0.24	0.24	0.18	0.24	3.48	3.28	2.55	3.35	0.19	0.14	0.19	2.49	1.84	2.43
25	0.28	0.27	0.21	0.27	3.36	3.19	2.55	3.23	0.20	0.15	0.20	2.33	1.84	2.28
30	0.32	0.31	0.24	0.31	3.24	3.09	2.55	3.12	0.21	0.16	0.21	2.19	1.84	2.14
35	0.36	0.35	0.27	0.35	3.13	3.00	2.55	3.01	0.21	0.18	0.22	2.05	1.84	2.00
40	0.40	0.39	0.31	0.39	3.02	2.91	2.55	2.91	0.22	0.20	0.23	1.92	1.83	1.88
45	0.45	0.44	0.35	0.44	2.92	2.83	2.55	2.81	0.23	0.22	0.24	1.80	1.83	1.76
50	0.50	0.49	0.40	0.48	2.82	2.74	2.55	2.71	0.23	0.24	0.24	1.69	1.83	1.65
55	0.56	0.54	0.45	0.53	2.72	2.66	2.55	2.62	0.24	0.26	0.24	1.58	1.83	1.54
60	0.62	0.60	0.52	0.59	2.63	2.58	2.55	2.53	0.24	0.28	0.25	1.48	1.82	1.45
65	0.68	0.66	0.59	0.64	2.54	2.51	2.55	2.44	0.24	0.31	0.25	1.39	1.82	1.36
70	0.74	0.73	0.67	0.70	2.45	2.43	2.55	2.36	0.24	0.34	0.25	1.30	1.82	1.27
75	0.81	0.80	0.76	0.76	2.37	2.36	2.55	2.28	0.24	0.37	0.25	1.22	1.82	1.19
80	0.88	0.87	0.86	0.82	2.29	2.29	2.55	2.20	0.24	0.41	0.25	1.14	1.82	1.12
85	0.95	0.94		0.88	2.21	2.22	2.12	0.24		0.24		1.07		1.05
90	1.02	1.02		0.94	2.13	2.16	2.05							
95	1.09	1.10		1.01	2.06	2.09	1.98							
100	1.17	1.19		1.07	1.99	2.03	1.91							
105	1.24	1.27		1.14	1.92	1.97	1.85							
110	1.32			1.20	1.85		1.78							
115	1.39			1.27	1.79		1.72							
120	1.47			1.33	1.73		1.66							
125	1.54			1.40	1.67		1.61							
130	1.62			1.46	1.61		1.55							

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Abstract.—We used hydroacoustic techniques to obtain biomass estimates of yellowtail rockfish, *Sebastes flavidus*, in a 100-km^2 area off the west coast of British Columbia, Canada. The purpose of our study was to estimate sampling variance and explore the effect of diel aggregation behavior on the precision of biomass estimates. A set of eight transects was sampled eight times: four at night, four during daylight. Although we observed a pronounced diel behavioral pattern of diurnal aggregation and nocturnal dispersion, we found no significant differences between nocturnal and diurnal estimates of mean biomass. Diurnal estimates showed a tendency towards higher variance, but the differences were not significant in most comparisons and were too small to influence survey design. The coefficient of variation of the eight observations for any individual transect ranged from 13 to 128%. The coefficient of variation in biomass for the whole survey area, based on repeating the set of eight transects eight times, was 13.9% and the estimate of mean biomass for the survey area was 1152 t. The observed diel behavioral patterns did not, in this study, produce different estimates of yellowtail rockfish biomass. Survey time might therefore be optimized without concern for this source of variance for this species.

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Diel vertical migration by yellowtail rockfish, *Sebastes flavidus*, and its impact on acoustic biomass estimation

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Yellowtail rockfish, *Sebastes flavidus*, are an important component of the British Columbia (B.C.) trawl fishery. Annual catches of 4000–5000 t represent about 20% of the total rockfish (*Sebastes* spp.) landings and over 5% of the total domestic trawl landings from the B.C. coast (Rutherford, 1996). The stock assessments for these species have typically relied upon population dynamics models tuned with catch-per-unit-of-effort indices (Stanley, 1993) or swept-area surveys (Leaman and Stanley, 1993). However, problems with both these methods have led us to investigate more direct methods.

Previous hydroacoustic work indicated that some of the trawl-caught rockfishes are aggregating species and that they are usually found associated with specific bathymetric features (Wilkins, 1986; Leaman et al., 1990; Kieser et al., 1992; Richards et al., 1991). Submersible observations and acoustic tagging of a small number of fish confirmed this association for yellowtail rockfish (Pearcy et al., 1989), although the acoustic tagging did not indicate consistent diel patterns (Pearcy, 1992). This aggregating behavior off the bottom in predictable locations suggests that this species may be a suitable candidate for hydroacoustic biomass estimation. However, because individual yellowtail rockfish stocks are thought to occupy large areas (Stanley, 1993; Stanley et al., 1994), such comprehensive hydroacoustic surveys would be costly and time-consuming. This accentuated the need for a prior study of fish behavior and sampling variance to assess the feasibility of such an approach and to optimize survey effort. We were also concerned about the impact of diel aggregating behavior on the precision and bias of biomass estimates (Olsen, 1990; Appenzeller and Leggett, 1992; Simmonds et al., 1992). Within the same genus, Richards et al. (1991) reported strong diurnal aggregation by Pacific ocean perch (*S. alutus*), and Wilkins (1986) has reported strong nocturnal aggregation by widow rockfish (*S. entomelas*).

We investigated these issues with an experimental survey in November 1991 in waters 10 km west of Vancouver Island, British Columbia, Canada (Fig. 1). The objective was to estimate yellowtail rockfish abundance within a small area and, in doing so, to examine the variance within and among transects. In addition, we wished to characterize diel patterns of behavior and document the effects of such behavior on the precision of the biomass esti-

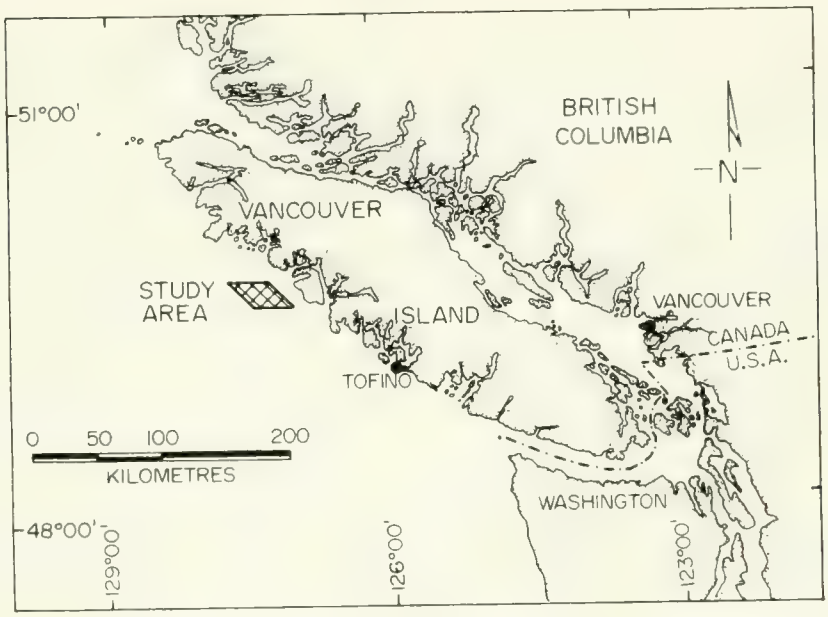

Figure 1

Location of study area off the southwest coast of Vancouver Island, British Columbia, Canada.

mates. In this report, we summarize our observations from this study and discuss the implications of the results to hydroacoustic survey design for yellowtail rockfish.

Methods

Study area

We first surveyed a 250-km^2 area along the shelf edge off Nootka Island to locate concentrations of rockfish (Fig. 1). This area produces 1000–3000 t of yellowtail rockfish per year (Rutherford, 1996). An initial grid included nine parallel transects 9–13 km in length and 2.8 km apart. They were oriented southwest to northeast, perpendicular to the isobaths. The southwestern end of the track lines extended well beyond the shelf break, whereas the shallower northeastern end extended onto the shelf to the 130-m isobath. This A series was covered during one 24-h period. The northern half of the A series showed the greatest concentrations of rockfish. From this northern area, we selected a B series of transects to conduct the study (Fig. 2). No further use was made of A-series measurements because the respective transects were not comparable with the B-series transects. The distance between transects was halved to 1.4 km, and the length of each was reduced to span depths from the 140-m isobath to just beyond the shelf break (180 m). The A series had shown that essentially all fish concentrations were between these limits. The B series was repeated in the same sequence (B9–B2) through four 24-h cycles to produce a balanced design of four diurnal and four nocturnal observations per transect. In addition to the acoustic estimates for the eight replicates of B2–B9, we selected B5 and B6 for continuous soundings, resulting in ten additional observations for these two transects.

The bottom topography of transects B2–B9, with the exception of B8, was characterized by one or two underwater cliffs They appeared to be 10–15 m high and followed a north–south axis through the study area, landward of the shelf break (Figs. 2–4). The transects were oriented perpendicular to the axes of the cliffs. At the southernmost transect (B9), the cliffs were approximately 1.5 km inshore of the shelf break. This distance increased to about 7.0 km by transect B2. The cliffs were found at a progressively shallower depth. This topographic feature is well known to fishermen as the "clay bumps" on the Nootka fishing grounds. Fishermen report that catches of yellowtail rockfish can be made year-round by towing bottom trawl nets in an east to west (shallow to deep) direction over the cliffs. Transect B5 corresponds to a commonly used commercial fishery tow (Figs. 2–4).

We excluded the results of transect B1 from our analyses. It passed over an extended underwater ridge such that the modal depth was less than 130 m rather than the targeted depth of 150 m. These depths are shallower than the November habitat

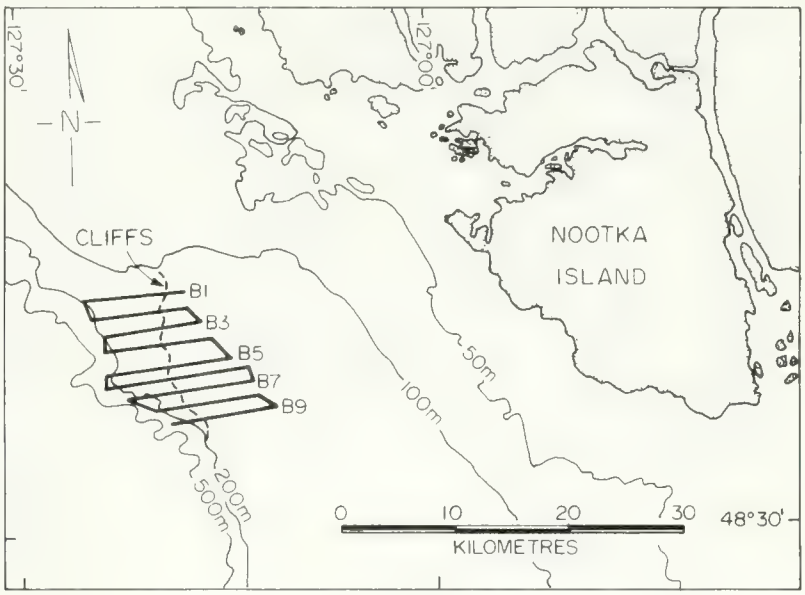

Figure 2

Area covered by the B-series transects and location of the shelf edge (200 m) and the cliffs in relation to the study area.

range for yellowtail rockfish (Nagtegaal, 1983). We also had to exclude the third of the four nocturnal replicates of transect B4. The vessel had to slow and change course to avoid traffic, leading to an unusable acoustic estimate. We used an average from the other three nocturnal estimates in our principal analyses to maintain a balanced ANOVA design. We also substituted a range of values in place of the missing value to examine the stability of the results.

Constant transects allowed us to compare behavior over the same location, but in doing so we sacrificed the improved statistical power we would have achieved with a stratified random design (Jolly and Hampton, 1991).

Time of the transect was classified according to the moment the vessel passed over the cliffs, the observed center of fish abundance. These times were then classified as diurnal or nocturnal according to the time of sunrise and sunset for Tofino, approximately 100 km southeast of the study area (Atmospheric Environment Service, Environment Canada).

Transect length

We derived two density estimates, based on a short and a long section from each completed transect, to examine the impacts of the choice of endpoints. For both sections and for each transect, we chose a standard beginning and end in relation to the cliffs (Fig. 3). The ends for the short sections of the transects were defined as the shoreward and seaward limits of the nocturnal dispersion of the cliff aggregations, judged visually from the echograms for all replicates. An individual transect required about one hour to complete. For these sections, the seaward end was inshore of the shelf break. The long sections used the same shoreward or shallow end, whereas the seaward or deep end was extended to a 180-m bottom depth. This depth incorporated the apparent deep-water limit of the shelf break aggregations (Fig. 3). The echograms for replicate transects (Fig. 3) differ in length because of differences in vessel speed over the ground. We calculated an average surface density (g/m^2) based on the constant length for each replicate of the short and long sections from all transects.

Hydroacoustic equipment and echo processing

Echo integration was used to estimate fish abundance in the survey area (Forbes and Nakken, 1972; Clay and Medwin, 1977; Foote, 1987; MacLennan and Simmonds, 1991). The calibrated echo integration system was operated from the Canadian Coast Guard Ship, *W. E. Ricker*. The acoustic processing equipment consisted of a BioSonics 38 kHz Model 101 echo sounder, BioSonics Model 111 chart recorder, BioSonics Model 121 digital echo integrator, PCM/VCR tape recording system, and auxiliary equipment. The transducer components included a towed body with a Simrad ceramic transducer and armored tow cable.

The echo integrator was programmed to analyze the return echoes for a series of depth strata (range slices) from the transducer to the bottom (Kieser et al., 1987). Bottom tracking was obtained with a 5-m bottom buffer. An echo integration sequence was completed every 60 pings (1 minute), and the measured echo intensities were stored on a personal computer. Echo integrator and chart recorder thresholds were set to 0.2 V; time-varied gain (TVG) was set to 20 log R. Thus all integrated echoes were displayed on the echogram. At this threshold level, noise was negligible at all depths of interest. Vessel speed was approximately nine knots.

The integrator output was processed with custom software to exclude extraneous signals from the ocean bottom, as well as noise and echoes from other unwanted sources in the water column.

A target strength (TS) of –32 dB/kg was used to convert the measured backscatter cross section to fish volume density (g/m^3) and fish surface density (g/m^2) estimates. This value was obtained from a review of the literature (Foote, 1987; Kieser, 1992); no *in situ* rockfish TS were available at that time. Only a relative TS was required because the study focused on the acoustic availability of rockfish and relative rather than absolute biomass and variance estimates.

Biomass estimates were obtained by extrapolating surface densities to cells that were bounded by lines equidistant between adjacent transects and by lines perpendicular to the transect and passing midway between measurements. An estimate of the total fish biomass for the area was obtained by summing the products of surface densities and cell areas.

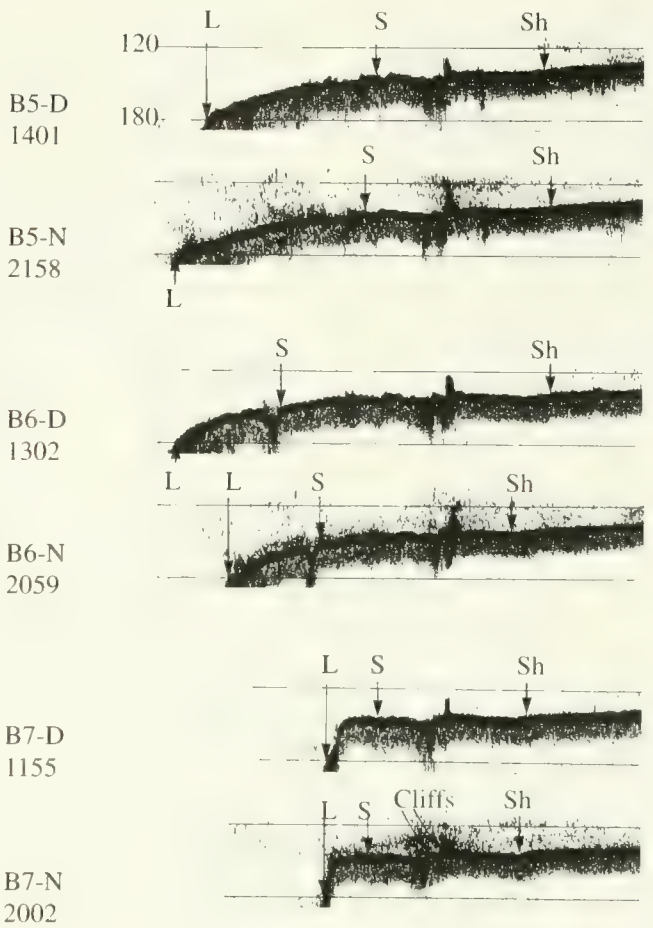

Figure 3

Diurnal (D) and nocturnal (N) echograms from transects B5, B6, and B7 for November 17. "Sh" identifies the shallow end of both long and short transects. "S" and "L" identify the deep ends of the short and long sections of the transects. Time shown represents the approximate time the vessel passed over the cliffs.

Fishing and sampling

We conducted three bottom trawl tows (Table 1). Two were conducted along the path of transect B5 and the other along transect B6. All three targeted diurnal aggregations at the cliffs. The tows ran from shallow to deep and were terminated at the seaward side of the cliffs, prior to encountering the aggregations near the shelf break. Planned additional bottom and midwater trawl fishing was curtailed owing to operational difficulties aboard the vessel.

Analysis of variance

Transect series 1, 2, 3, and 4 were conducted 17–18, 20–21, 22, and 24–25 November (Table 2). We initially tested for diel, transect, and series effects with a three-factor ANOVA:

$$\overline{D}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \varepsilon_{ijk},$$

where $\overline{D}_{ijk}$ = surface density for transect i, day or night j, and observation (or series) k;
μ = the overall mean;
α_i = the transect effect;
β_j = the diel effect.
γ_k = the influence of the date (series); and
ε_{ijk} = the error term, normally distributed with a mean of 0 and variance of σ^2.

To test whether diel variances were heterogeneous, we conducted a one-way randomization ANOVA limiting the factors to the diurnal-nocturnal effect. We conducted this test on a scaled version of the observations. Because it was obvious that the variance

among transects was, in part, proportional to the mean, we removed the transect effects by scaling all the observations. Each observation was multiplied by the overall mean for the data set (n=64) divided by the mean for all eight observations (diurnal and nocturnal) of the transect. Thus the variation in the data set was reduced to the scaled "within transect" and diel effects.

Following examination of the balanced treatment of all transects, we examined the observations for transects B5 and B6 (Table 3). These data included observations from the four series as well as additional nonpaired observations. The two transects were examined separately. Homogeneity of variance between diel periods was examined by using an F-ratio test.

We used nonparametric randomization tests (Manly, 1991) to examine the sources of variance owing to concern about the small sample sizes, non-normality, and heterogeneity of variance. In particular, we hypothesized that variance among repeated transects would be proportional to the biomass estimates and, owing to the extreme densities and localization of the diurnal aggregations, that diurnal variance would be significantly greater than nocturnal variance.

Randomization involves resampling without replacement from one parent population. The observed value of the response statistic (for example, mean diurnal biomass minus mean nocturnal biomass) is compared with a large number of responses generated by treating all observations (diurnal and nocturnal) as coming from one parent population. Each of 4999 resamplings randomly allocates the observations into two groups, each time simulating new diurnal and nocturnal sets. The observed difference in mean biomass is then compared with the 4999 simulated differences. If the observed difference in biomass is significant (α<0.05), then the observed difference should be greater than 95% of all the simulated differences.

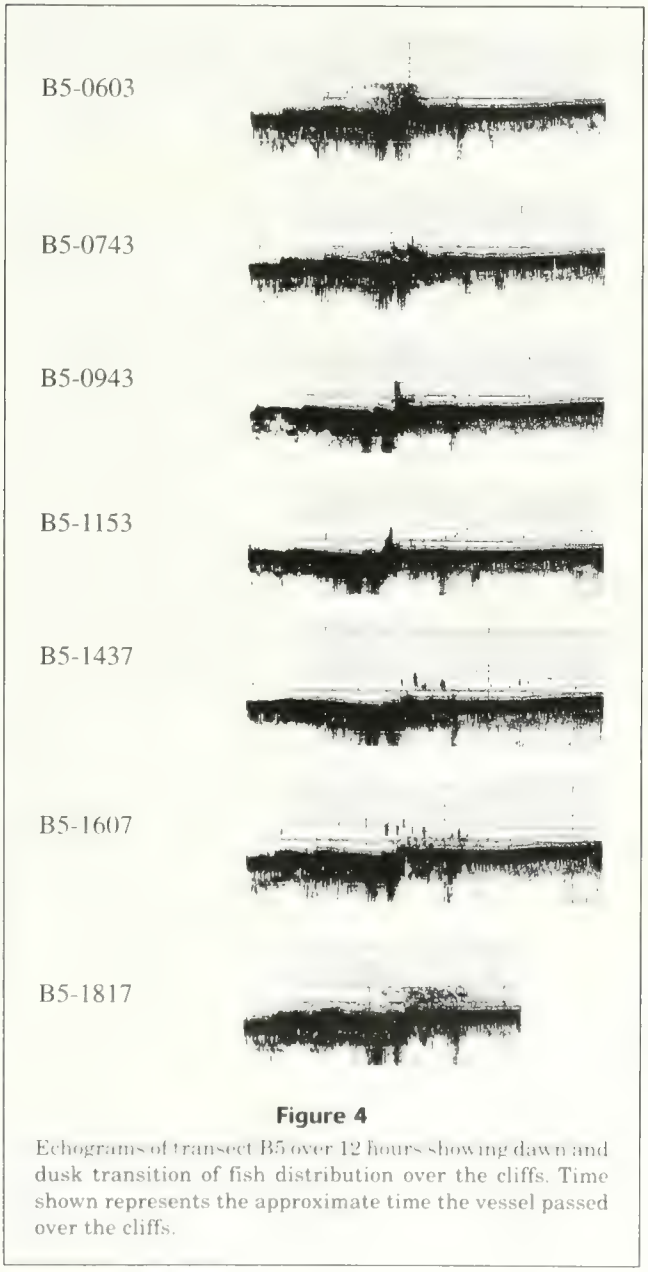

Figure 4

Echograms of transect B5 over 12 hours showing dawn and dusk transition of fish distribution over the cliffs. Time shown represents the approximate time the vessel passed over the cliffs.

Results

Fish behavior and species composition

Four aggregation types were observed on the echograms. Each was associated with a different habitat. The first, our targeted group, was located near the cliffs over depths of 150–160 m (Fig. 3). These dense schools were located near the bottom during each day, then the fish dispersed vertically and horizontally at twilight. By early nighttime, the scattered targets were distributed from 80 to 150 m. The diel cycle was completed by downward migration and rapid reformation of schools at dawn.

With the exception of benthic species like flatfish, which produce a negligible contribution to the acoustic measurement, the species composition in the catch from this aggregation type was over 85% yellowtail rockfish in the three tows (Table 1), indicating that this species dominated in the diurnal aggregations targeted near the cliffs. The continuous transition from day to night distributions (Fig. 4) implies that the nocturnal aggregations were also yellowtail rockfish, but it was not possible to confirm this assumption during the cruise. Subsequent discussions with fishermen familiar with nighttime trawling in the area supported the assumption that the nocturnal

Table 1

Catch composition (%) by weight and by species from diurnal bottom trawl tows ("tr" signifies trace, <0.05%).

	Tow			
	1	2	3	Total
Rockfish				
Silvergray rockfish (*Sebastes brevispinis*)	3.8	4.6	7.7	4.0
Widow rockfish (*S. entomelas*)	0.9	0.5	1.3	0.8
Yellowtail rockfish (*S. flavidus*)	88.2	83.2	38.5	85.9
Bocaccio (*S. paucispinis*)	7.1	2.8	tr	6.2
Other rockfish (*S.* spp.)	tr	tr	3.8	0.2
Other species (with swimbladders)	tr	0.3	2.6	0.1
Other species (without swimbladders)	tr	8.4	46.2	2.8
Total catch (kg)	1989	393	78	2460

Table 2

Biomass estimates (t) for the short and long sections of the transects ("na" indicates not available, measurement aborted owing to vessel traffic).

	Series							
	1		2		3		4	
Transect	Short	Long	Short	Long	Short	Long	Short	Long
Day								
2	93	119	65	70	96	104	170	188
3	162	162	228	232	114	118	103	106
4	98	99	37	50	126	134	46	60
5	124	130	84	92	124	136	92	124
6	424	448	520	522	32	32	396	402
7	148	148	39	40	186	194	111	116
8	4	4	58	58	161	208	18	20
9	187	187	209	278	296	345	118	123
Night								
2	181	200	112	124	116	123	59	68
3	92	113	152	166	85	90	124	134
4	56	112	77	103	na	na	74	84
5	128	230	112	162	128	180	92	100
6	156	216	150	180	476	512	128	144
7	198	212	114	138	224	235	229	241
8	185	224	142	169	131	173	146	157
9	76	126	178	202	240	357	168	208

targets would probably have been yellowtail rockfish. Commercial fishery records from these fishing grounds consistently indicate a predominance of yellowtail rockfish in midwater and bottom trawl tows.

The daytime tows support the assumption that the aggregation over the cliff was that of yellowtail rockfish, and the nocturnal dispersion of these aggregations is obvious from the night transects. These aggregations appear almost as dense as the bottom on our daytime echograms. The cliffs can be identified only in the echogram during the night (Figs. 3 and 4). We are not, however, suggesting that all fish in the transect were yellowtail rockfish, nor are we suggesting that the diurnal aggregations at the cliff represented all the yellowtail rockfish that were present in the transects. The nocturnal "cloud" may have included fish that were close to the bottom but not adjacent to the cliffs.

Figure B6-N indicates that there was some movement from off the edge onto the long and short ver-

Table 3

Biomass estimates (t) for the short and long sections of B5 and B6 (all observations).

			Series										
	Type	Transect	—	1	2	3	4	—	—	—	—	—	—
Day	Short	5		124	84	124	92	64	182	116	610	38	
	Long	5		130	92	136	100	172	182	132	632	332	
	Short	6		424	520	32	396	300	500	312	92		
	Long	6		448	552	32	402	308	508	320	124		
Night	Short	5	136	128	112	128	92	28	170	120	102	132	
	Long	5	188	230	162	180	124	28	212	156	140	288	
	Short	6	170	156	150	476	128	238	212	240	176	294	244
	Long	6	192	216	180	512	144	272	256	262	232	244	280

sions of the transect, suggesting some added contamination; however most of the backscatter was still concentrated near the cliffs.

A second aggregation type was represented by the schools observed at the shelf break, 10–20 m deeper than the base of the cliffs (Fig. 3). These schools, although exhibiting diel behavior similar to that of the first group, remained closer to the bottom during daytime. The greater depth of the aggregations (160–180 m), their closer proximity to the shelf edge, and their stronger bottom affinity suggested to us, as well as to various fishermen with whom we consulted, that these aggregations probably consisted of a combination of Pacific ocean perch (*S. alutus*), canary (*S. pinniger*), redstripe (*S. proriger*), sharpchin (*S. zacentrus*), and silvergray (*S. brevispinis*) rockfish (Leaman and Nagtegaal, 1982, 1986; Leaman et al., 1990).

The third and fourth target types included small schools or individual targets within the shallow end of the transects and scattered distributions over much deeper water beyond our transects and the shelf edge. The shallower signals were thought to be plankton or small fishes. Fishermen reported that attempts to fish on these aggregations were unsuccessful and suggested that the source of the signals was too small to be retained by their gear. No *in situ* target strength measurements were conducted. Signals in deeper water, off the edge of the shelf break, have been shown in other studies to be a deep plankton layer or hake (*Merluccius productus*) (Saunders[1]). Signals close to the slope off the edge could also be generated by side echoes.

Analysis of variance

The randomization tests provide the percent of the random re-orderings that exceed the value of the observed response. Statistical significance is assumed when fewer than 5% of the re-orderings exceed the observed response. The three-factor ANOVA indicated for both short and long transect sections (Table 4) that

Table 4

Results of three-factor randomization ANOVA (df=degrees of freedom; **>1% significance level). Percentages indicate the % of 4999 random combinations of the observed data which resulted in a difference between treatments greater than the observed difference.

		% greater than observed	
Factor	df	Short section	Long section
Diurnal and nocturnal	1	87.94	47.40
Transect	7	**0.08	**0.08
Series	3	80.50	66.89
Error	53		
Total	64		

1 there was no significant difference in mean biomass between night and day;
2 there was a highly significant difference in mean biomass among transects; and
3 there was no significant difference in mean biomass among different series (over time).

Bartlett's test for homogeneity of variance indicated no significant difference between the variance of diurnal and nocturnal observations, although the trend was towards greater diurnal variance (Table 5).

We repeated the same basic analysis using the larger but nonpaired set of observations for transects B5 and B6 (Table 3). Each transect was analyzed separately to test for significant differences between diurnal and nocturnal mean biomass and for homo-

[1] Saunders, M. 1991. Pacific Biological Station, Nanaimo, B. C., Canada V9R 5K6. Personal commun.

Table 5

Results of Bartlett's test for significant difference between variance of diurnal and nocturnal observations (χ^2 for P=0.01 is 2.706; χ^2 for P=0.05 is 3.841).

	Short section	Long section
χ^2	2.45	2.23

geneity of variance between the two diel periods (Table 6). These data included the observations from the comparisons above; therefore, the data sets and tests are not independent of the main ANOVA.

Results for the short segments for B5 and B6 also showed no significant differences between mean nocturnal and diurnal biomass. However, unlike the results of the expanded B5 data set and the original all-transect test, diurnal variance for B6 was significantly higher than nocturnal variance for this transect.

Missing observation

The impact of using an average value (69 t) for the missing nocturnal observation was examined by conducting the randomization tests with minimum and maximum values of 56 t and 76 t for the nocturnal observations from B4. The alternate values had a negligible impact on the results.

Nocturnal dispersion beyond the shallow end of the transect

During one night series, the echograms indicated that the cliff aggregations dispersed beyond our empirically chosen shallow endpoint in transects B5–B9. We therefore slightly underestimated the nocturnal abundance of the cliff aggregations this one night. We re-analyzed the biomass for these transects with the new endpoints and then repeated the statistical analyses for the B2–B9 and B5–B6 series only. The changes to the one night's observations did not affect the results significantly.

Variance in transect and total biomass estimates

Independent total biomass estimates for the study area were estimated as the sum of the transect biomass estimates from each series (Table 7). The overall average was 1152 t with a CV of 13.9% among series for the short sections. For the long sections, the average was 1329 t with a CV of 15.4%. The within-transect CVs ranged from 16.6% to 65.8% for the eight transects (short sections).

Table 6

Results of comparison of expanded observation set from transects B5 and B6 (* indicates > 5% level of significance). Percentages indicate the % of 4999 random combinations of the observed data which resulted in a difference between treatment means greater than the observed difference in means.

		% greater than observed	
Transect	Factor	Short section	Long section
5	Diurnal and nocturnal	35.79	22.54
	F-ratio	16.08	15.90
6	Diurnal and nocturnal	5.28	10.08
	F-ratio	16.10	1.60*

Table 7

Coefficients of variation of biomass estimates ($\hat{B}$) among transects and series (short and long sections).

		Short section		Long section	
Area	n	$\hat{B}$(t)	CV%	$\hat{B}$(t)	CV%
Total area					
Day	4	1167 t	7.7	1256	7.9
Night	4	1137 t	19.8	1402	19.3
Day+ Night	8	1152 t	13.9	1329	15.4
		CV% range		CV% range	
Within transects					
Day	4	19.8–117.8		19.0–128.5	
Night	3–4	14.9–73.0		14.3–64.1	
Day+ Night	7–8	16.6–65.8		31.4–68.1	
Among transects					
Day	4	54.3–106.7		58.4–100.6	
Night	4	24.5–67.3		20.6–62.2	

Aglen (1983) derived an empirical formula for predicting the CV based on the ratio of linear distance surveyed (L) over the square root of the surveyed area (A), which he called the "degree of coverage" or DOC:

$$Predicted\ CV = 0.5\left(\frac{L}{\sqrt{A}}\right)^{-0.41}.$$

The variance among the eight series replicates of the area were significantly less than the predicted value

from Aglen's formula whereas the variance for the combined area of B5 and B6 was higher (Table 8). In both cases, the observed variance among surveys was typical of acoustic surveys.

Discussion

We have assumed that the dominant part of the acoustic signal selected from the short transects represented yellowtail rockfish, a conclusion supported by fishing results and the continuity on the echograms between diurnal and nocturnal distribution. The longer sections of the transects, which indicated about 16% (5–30%) more total biomass, probably included other species of deeper-dwelling rockfishes.

Yellowtail rockfish share with other species a diel pattern of diurnal schooling and nocturnal dispersal (Simmonds et al., 1992). We observed that the schools reform at dawn near a minor but nearly continuous topographic feature that crosses the study area on a north–south axis. The strong and persistent affiliation of yellowtail rockfish with this small cliff is consistent with long-term commercial fishing records at this location. The diurnal schools are near the bottom at dawn then rise slowly during the day, dispersing at dusk. This is congruent with fishermen's observations that early morning is the most productive time for bottom trawling for this species. The fidelity to topographic features is consistent with reports of Pearcy (1992) and Carlson and Haight (1972). Pearcy's reports on acoustically tagged specimens includes an example of "homing" near to the original capture sites, even as far as 2 nmi overnight.

Because we conducted the study at only one time of year, we could not examine how diel behavior would vary with season. Fishermen report that yellowtail rockfish occupy the "cliffs" at all times of year. They also report that the dawn tows are the best fishing on a year-round basis. We would suggest that if diel vertical movement is triggered by or at least associated with light intensity at depth, then the effect would be more obvious during summer months when light intensity increases and the twilight period shortens. It might also be more dramatic on brighter days.

The diversity of species, especially near the shelf edge, illustrates that a difficult issue facing acoustic assessment of rockfish will be species identification. This process will be complicated by the difficulty of trawling much of the habitat. Our study was based on single-beam and single-frequency acoustic observations. Encouraging results on species identification have been obtained by more advanced acoustic analysis of individual fish schools (Kieser and Langford, 1991; Scalabrin and Masse, 1993), comparison of day and night survey data (Gerlotto, 1993), and multifrequency and wide band observations (Simmonds and Armstrong, 1990; Zakharia, 1990). In this context, innovative transducer design and deployment will be important to obtain more detailed acoustic data from individual fish and schools near the bottom.[2] Supplemental information on habitat and depth preference by species, perhaps developed from simultaneous use of submersible devices or side-scan bathymetry, may help to estimate species' proportions (Richards et al., 1991).

Diurnal versus nocturnal density and biomass estimates

Although the echograms showed differences in diel distribution for yellowtail rockfish, they did not indicate the extreme densities which lead to acoustic shadowing (Foote, 1990). In contrast to other studies (summarized in Appenzeller and Leggett, 1992), which report higher density estimates from night observations, our day and night estimates were similar. We conclude that, for yellowtail rockfish, diel behavior patterns do not bias hydroacoustic biomass estimates. It remains possible, however, that the similarity between diel periods is purely fortuitous in that the various factors that could affect estimation, such as movement in and out of the study area

[2] Dalen, J., and H. Bodholt. 1991. Deep towed vehicle for fish abundance estimation, concept and testing. ICES Council Meeting (CM) 1991/B:53, 13 p. [Mimeo.]

Table 8

Observed coefficient of variation (CV) of biomass estimates from short section in comparison with predicted CV from formula by Aglen (1983). Sample size, n, is the number of replicate coverages of either the area represented by transects B5 and B6, or the overall area of B2–B9.

Transect	n	Section	Distance (km	Area km²	DOC	Predicted CV%	Observed CV%	Mean estimated biomass (t)
B5-6	19	Short	11.0	15.2	2.82	32.7	48.0	397
B2-9	8	Short	39.6	55.5	5.33	25.2	13.9	1152

or diel variability in tilt angle, may simply have cancelled each other out.

We assumed that there are no diel changes in fish target strength. Such changes have been observed for other species and have been linked to swimming behavior or mean tilt angle (Miyashita et al., 1995; Buerkle and Sreedharan, 1981; Olsen, 1990; Misund, 1997). Target strength variation between night and day may be smaller for yellowtail rockfish because these fish tend to remain in the same general depths. They are not moving from the bottom to surface waters and therefore not encountering large relative changes in pressure.

The observed diel behavior of increased aggregation during the day led us to hypothesize that variance in biomass should be greater for diurnal observations. We observed that yellowtail rockfish move towards the cliffs at dawn. We assumed that they would concentrate further along that narrow band to produce discrete schools. We viewed the nocturnal distribution as a relatively dispersed band (three-dimensional cloud) of individuals in the general vicinity of the cliffs. We assumed that the diurnal distribution, which lay along the orientation of the cliff, would be a much narrower string of individual schools and hence of highly varying density, perhaps to the extent of approximating a "beaded pattern" of distinct schools following the length of the cliff. We expected that diurnal estimates derived from transects that pass perpendicular to the cliffs would be highly variable because the path of the acoustic beam could range from "missing entirely" to "completely ensonifying" a dense school.

We found that, for the short transect version of the all-transect data, the variance of diurnal biomass estimates was not significantly greater than that of nocturnal biomass estimates. Diurnal variance was significantly higher in the expanded set of the B5–B6 set of observations but only for the long version of transect B6.

The weak or mixed indication of higher diurnal variance implies that the apparent aggregation towards the cliffs, evident in the echograms, is not matched to the same degree by aggregation along the axis of the cliffs. We expected discrete diurnal schools following the axis of the cliffs. This tendency to aggregate into a continuous band of fish along the cliffs, as opposed to discrete schools, may be unique to this area where there is a longitudinal topographic feature along the preferred depth. In areas of the coast lacking in such a linear feature, fish may tend to aggregate over a specific point, such as a pinnacle, producing greater daytime variance among estimates of biomass. Results of this experiment, however, do not support the hypothesis that estimates from the dispersed condition will show less variance for yellowtail rockfish. The similarity in variance between nocturnal and diurnal periods indicates that no substantial gains in efficiency or precision can be achieved by sampling during one or other of the diel periods.

The among-transect variance overwhelms the other sources of variance even within a small coastal area. From the perspective of two-stage sampling (among-transect or within-transect variance), precision of the overall estimator is reduced by allocating sampling effort in proportion to variance contributed by each stage. Because among-transect variance is much greater, survey design should maximize the number of transects at the expense of replicating transects. The only exception to this principle would arise when the cost of replicate samples is much lower. Because the cost of collecting a replicate transect estimate is almost equal to that for an additional transect over the scale we are considering, it would be more efficient to maximize the number of different transects.

By repeating the survey eight times, we were able to determine the variance of the biomass estimate directly rather than by inferring it indirectly through geospatial analysis of "within" variance (Petitgas, 1993). This calculation of "among" survey variance follows from work by Williamson (1982), who resampled from the individual samples averaged over one minute within a transect, and by Robotham and Castillo (1987), who bootstrapped cumulative transect observations as we did. There is no question that a formal investigation of the spatial impact on variance would require treatment at the granular level of the observations, which the geospatial methods provide. These procedures also facilitate an investigation of the impact of additional explanatory variables and development of model-based inference. However, the requirements of our study were realized by the simpler transect-based analysis.

Total biomass estimate and survey design

The overall biomass estimate of 1152 t for the study area appears consistent with overall coastal biomass estimates of 50,000–60,000 t for a stock that is assumed to extend from the study area to the border of B.C. and Alaska (Stanley, 1993). The fact that the overall coefficient of variation among the eight series for the study area was under 14% is encouraging and better than that predicted from the formula of Aglen (1983). This precision may not, however, apply to all rockfish species. Wilkins (1986) found that the CV for widow rockfish was 2–3 times higher in spite of a more comprehensive estimation procedure that included the use of side-scan sonar in conjunction with echosounding. We can also expect

greater variation if repeated estimates were conducted at greater time intervals.

Over a one-week period and an area of over 100 km^2, we have demonstrated precision (CV=15%) in acoustic biomass estimates that is acceptable in a stock assessment context for yellowtail rockfish. Variance among replicated transects is low enough that survey effort can be distributed to maximize the number of different transects, either to increase the area of the survey or the density of coverage. We have shown that a survey of yellowtail rockfish can be conducted throughout the diel cycle and thus reduce survey costs.

This study also indicates that yellowtail rockfish can aggregate within a well-defined bathymetric range near topographic features. If these tendencies are consistent over the whole range of this species, they may provide the basis for stratification and possible further gains in efficiency. Our results indicate that a simple systematic transect design with transects oriented perpendicular to the long axis of the fish concentrations (the edge of the continental shelf) is a satisfactory choice for the elementary sampling distance unit (ESDU) (Simmonds et al., 1992; Simmonds and Fryer, 1996). If the preferable depth range is narrow over most of the coastline and the survey must thus cover a long narrow corridor, then a systematic zig-zag would be preferable (Simmonds et al., 1992).

The affiliation of yellowtail rockfish with a minor topographic feature within a depth range indicates that the density distribution of yellowtail rockfish is "nonstationary," in that the densities will not be randomly distributed in a study area or stratum, even after bathymetric stratification (Simmonds et al., 1992). This is an important characteristic of the species and should be noted if more advanced survey design and analysis procedures, such as geostatistical spatial averaging and cokriging, are to be investigated (Foote and Stefansson, 1993; Marcotte, 1991).

Although the results of the experiment support the potential for acoustic estimation of this species, the generality of the conclusions will have to be tested over a larger scale and more varied habitat. The study site was chosen carefully to minimize the unknowns, in particular the presence of other species. The hypotheses will have to be re-examined over different depths and topography. It is also possible that the annual cycle of maturation, mating, and parturition for these livebearing fish may be associated with different behavior.

Acknowledgments

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Variability in reactions of Pacific harbor seals, *Phoca vitulina richardsi*, to disturbance

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Abstract.—Disturbances to harbor seals, *Phoca vitulina richardsi*, during 1991 and 1992 pupping seasons were observed at Puffin Island, Clements Reef, and Skipjack Island in Washington state. Harassment (≥ one seal entering the water) of seals ashore was common (≥71% of survey days) and primarily caused by powerboat operators approaching to observe seals. Recovery (number of seals on a haul-out site returned to preharassment levels) following a harassment was less at Puffin Island (19%) than at Clements Reef (54%) and Skipjack Island (45%). Additionally, seals were more vigilant ($P<0.003$) at Puffin Island than at the other two locations. These results indicated that seals at Puffin Island were less tolerant of disturbance than seals at other sites. This could possibly be attributed to a greater ($P<0.05$) percentage of pups ashore (17%) than at Clements Reef (3%) and Skipjack Island (3%). Because of this, we expected that powerboats would disturb seals from greater distances at Puffin Island. To test this, we used a theodolite to determine distance between seals and an approaching vessel at Puffin Island and Clements Reef. There was, however, no significant ($P>0.05$) difference in distances at which disturbances occurred. The most notable difference in distance of disturbance was between initial and subsequent harassments during a haul-out period. Those seals remaining or returning to shore after a harassment were more tolerant of powerboats, allowing significantly ($P<0.05$) closer approaches than those initially harassed. Seals detected (head raised and oriented toward the potential disturbance) a powerboat at a mean distance of 264 m, and harassments occurred when boats approached, on average, to within 144 m. Results of this study exemplify the variability in reaction to disturbance and the necessity for considering these differences for minimizing disturbance.

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In many locations, disturbance is an important factor affecting the haul-out patterns of harbor seals, *Phoca vitulina*. Disturbance is defined as any activity that alters normal behavior. In the United States, disturbance of marine mammals by humans is regulated by the Marine Mammal Protection Act of 1972. In contrast to pelagic marine mammals, changes in the behavior of pinnipeds on haul-out sites related to disturbance is relatively simple to measure. Long-term effects of disturbance, however, are often difficult to assess.

The effects of disturbance may be quite mild or may cause displacement and even mortality. Bighorn sheep (*Ovis canadensis*) and white-tailed deer exposed to snowmobile traffic have shown increased heart rate but no visible change in behavior (MacArthur et al., 1982; Moen et al., 1982). Humpback whale (*Megaptera novaeangliae*) female-calf pairs in Hawaii have avoided nearshore areas of intense human recreational activities (Salden, 1988; Glockner-Ferrari and Ferrari[1]). Disturbance-related mortality in harbor seals can result from stampeding and pup abandonment (Johnson[2]). Disturbance from low-flying aircraft may have caused mortality of more than 200 (10%) harbor seal pups on Tugidak Island, Alaska, in 1976 (Johnson[2]).

In addition to aircraft, sources of disturbance include boats, seismic exploration, pedestrians, kayakers, and natural predators (Renouf et al., 1981; Laursen, 1982; Allen et al., 1984; Terhune, 1985; Richardson et al., 1995; Moss, 1992; Kroll, 1993; Johnson[2]; Murphy and Hoover[3]; Calambokidis et al.[4]; and others). Allen et al. (1984) reported that harbor seals on a haul-out site in Bolinas Lagoon, California were disturbed by humans on 71% of survey days; most disturbances were caused by nonmotorized boats (primarily canoes). Humans, primarily boat operators, were the most common cause of harassment to harbor seals on Pro-

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tection Island (Kroll, 1993) and Woodard Bay (Calambokidis et al.[4]), Washington. Sources of disturbance to harbor seals ashore at Gertrude Island, Washington, were mainly unidentifiable; however, of detectable causes, human activities and coyotes were the most common (Moss, 1992).

Reaction to disturbance may vary among harbor seal groups within an area (Terhune and Almon, 1983) and according to disturbance sources (e.g. powerboats vs. canoes and kayaks; Calambokidis et al.[4]). This variability may be attributed to different levels of tolerance among age, sex, or reproductive status of harbor seals. Reaction to different causes of disturbance may vary with exposure to particular sources, eventually resulting in greater avoidance or tolerance. In any case, results of previous studies indicate that reaction to disturbances vary within and among regions, although little quantitative evidence exists.

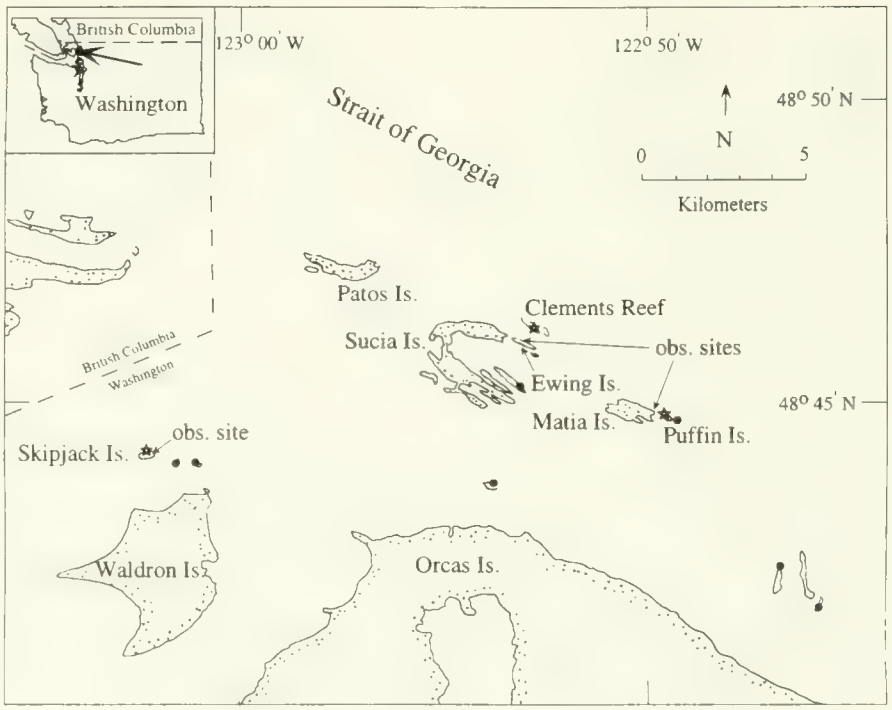

Figure 1

Locations (★) of harbor seal haul-out sites observed at Clements Reef, Puffin Island, and Skipjack Island during 1991 and 1992 pupping seasons in the San Juan Islands, Washington. Dots (•) indicate other haul-out sites in the area.

In this study, we collected data to evaluate the extent of disturbance to harbor seals at haul-out sites in the northern San Juan Islands. Our objectives were to determine 1) if human-related activities were the primary source of disturbance; 2) if recovery varied between flood and ebb tides and was similar among the three haul-out sites (one location was a pupping area); 3) if vigilance characteristics differed among haul-out sites; 4) if the response to harassment was similar for pups and for adults and subadults; and 5) if the mean distance between harbor seals and a boat causing a disturbance varied within and among haul-out sites and, if so, to determine potential causes of this variability.

Methods

Study area

The study area was located in the northern San Juan Islands, Washington (Fig. 1). This area is characterized by numerous islands, a tidal range of 3.6 m, strong currents (maximum of 7.7 km/h), and a rocky shoreline. Haul-out sites of harbor seals, which include reefs and rocky intertidal zones of islands, are numerous but typically are used by fewer than 100 animals. During this study, observations were conducted at Clements Reef, Puffin Island, and Skipjack Island (Fig. 1).

Observations of haul-out sites

Ground-based surveys of harbor seals were conducted at Clements Reef (n=13), Puffin Island (n=9), and Skipjack Island (n=8) from 2 July to 19 August 1991. In 1992, surveys were conducted between 24 June and 10 September 1992 at Clements Reef (n=21) and Puffin Island (n=18). Skipjack Island was not surveyed during 1992 to allow increased sampling effort at the other two sites. Seals at each location were observed at least twice a week (one observer per site). Seals at Clements Reef were viewed from Ewing Island (Fig. 1), approximately 0.55 km away. Seals on the northwest end of Puffin Island were viewed from the southeast corner of Matia Island, 0.38 km away (Fig. 1). Observer heights above zero tide level were 10 m at Clements Reef and 13 m at Matia Island. The observation point on the northeast side of Skipjack Island was directly above (23 m) the haul-out site (Fig. 1).

Observations of harbor seals began one to three hours before low tide and ended three to seven hours after low tide (when <50% of the maximum number of seals counted during that tide cycle remained ashore).

Seals were viewed with 22× and 15–60× spotting scopes. Scan surveys (Altmann, 1974) were conducted at ten minute intervals throughout the observation period. During each half-hour period, the first scan was a count of all seals, the second scan included size structure (number of harbor seal pups and subadults and adults), and the third scan was used to quantify vigilance of seals (head up, alert but not oriented toward a disturbance source) and sources of disturbance (within 1.0 km of the haul-out site). Counts of size structure included only those individuals that could be assigned a given category (e.g. seals were not included if only a flipper was visible as in the first scan).

Counts from these scans were used to determine how many seals entered the water following a disturbance and when recovery had occurred. Recovery was measured by the increase in number of harbor seals on the haul-out site after harassment. Recovery was divided into four categories: 1) full recovery (number of seals ashore after harassment returned to preharassment levels); 2) partial recovery (number of seals ashore increased after the harassment, but did not reach preharassment levels); 3) no recovery (number of seals ashore did not increase after harassment); and 4) no chance to recover (number of seals ashore never increased after harassment owing to repeated disturbances or rising tide washing over the haul-out site). Because animals were not marked, full recovery did not imply that individuals returning to shore were necessarily the same ones that were harassed, but partial and no recovery did indicate certain individuals did not return to the haul-out site.

Terhune (1985) and da Silva and Terhune (1988) reported that the number of vigilant harbor seals was dependent on group size. To eliminate the potential effect of group size on vigilance, the original data were subsampled to produce subsets of equal group sizes. Therefore, a single value is not presented for a site because it varies with each comparison.

Data were collected for every potential source of disturbance that approached the haul-out site. Sources were divided into the following categories; airplanes, powerboats (including sailboats under motor power), sailboats, kayaks and canoes, people, bald eagles (*Haliaeetus leucocephalus*), unknown, or other. Vessel speed was classified as underway fast (creating a breaking bow wake), underway slow (nonbreaking bow wake), and drifting (motor not in gear or turned off). Harbor seal reactions to a disturbance were categorized as 1) detection: ≥1 seal with head raised and oriented toward potential disturbance source; 2) alarmed: ≥1 seal moved from its resting place, but did not enter the water; and 3) harassed: ≥1 seal entered the water.

Positions of an approaching vessel were monitored by using a Nikon NT2A or Pentax TH20D theodolite. Bearings to the approaching vessel and seals exhibiting disturbance reactions were recorded. The distance from theodolite to vessel or seal was calculated by using the tangent of the vertical angle from the theodolite and height of the theodolite above the water. The distance between vessel and seals was calculated by using the Law of Cosines that incorporates distances between theodolite and vessel and theodolite and seals and by using the horizontal angle between the vessel and seals (from theodolite). Height of the theodolite above water was measured directly or estimated from a cosine prediction of tide height (San Juan Current and Tide Tables, published by Island Canoe, Bainbridge Island, Washington). The tidal constituent used was Port Townsend, Washington, with a correction for Echo Bay, Sucia Island (approximately 1 km from Ewing Island and 6 km from Puffin Island). The observation point at Ewing Island (for Clements Reef surveys) was near a vertical rock ledge, which allowed the observer to measure theodolite heights above water level (using a tape measure with float attached). Direct measurement of height above water was accurate to approximately 0.1 m. Direct measurement was not possible at Puffin Island; therefore, theodolite heights above water level were based on tide height predictions, which were accurate to approximately ±0.3 m. Error in theodolite locations was less than 10 m; accuracy was based on calibration with fixed objects (e.g. buoy or island).

Analyses

Results of statistical analyses were considered significant at $\alpha = 0.05$. Mean percentage of pups among the sites was compared by using analysis of variance (ANOVA) with arcsine transformation. A Tukey multiple comparison test was used for significant ANOVA results (Zar, 1984; Day and Quinn, 1989). To test whether pups were less tolerant of disturbance than adults, the frequency of positive and negative changes in the proportion of pups ashore before and after a harassment was compared by using a chi-square goodness-of-fit test (data were combined from all sites). Percentage of vigilant seals was compared between sites by using Mann-Whitney U tests (separate two-sample tests were conducted owing to random subsampling to control for group size). Differences in distance of disturbance among powerboat approach speeds were tested with Mann-Whitney, t, and Kruskal-Wallis tests. Significant differences in distance of disturbance among categories of detection, alarm, and harassment were detected with

Table 1

Summary of numbers of harbor seals using haul-out sites and primary disturbances occurring during the pupping season of 1991 and 1992 in the northern San Juan Islands, Washington.

	Puffin Island	Clements Reef	Skipjack Island
No. of seals (range)	50–125	125–275	50–125
% pups (SE)	17% (1.1)	3% (0.3)	3% (0.4)
% of days with harassment (n)	77% (27)	71% (34)	88% (8)
No. of harassments observed	64	91	24
% of harassments caused by powerboats	42%	76%	46%
Unknown[1]	19%	2%	38%
Bald eagle	16%	2%	0%

[1] No disturbance source was detectable by the observer.

ANOVA with square root transformation. Initial versus subsequent disturbances were compared within each disturbance categories with t-tests. Randomization statistics (Resampling Stats, Inc., 1995) were used in calculation of power to detect significant differences.

Results

Clements Reef was the largest haul-out site with the greatest number of seals. Puffin Island, however, had the greatest number of pups, the pups representing a significantly (F=97.6, P<0.01) greater percentage of the total number of seals ashore in comparison with Clements Reef (Table 1). The study area on Puffin Island appeared to be an important area for female-and-pup pairs and thus may explain some of the observed differences in reactions to disturbance.

Harassments of seals occurred during at least 71% of the survey days. The primary cause of disturbance was powerboats (Table 1). Most of these (74%, n=96) involved boat operators approaching haul-out sites to view seals. The second most common category of disturbance was unknown (no source was visible or audible to the observer) and was most prevalent at Skipjack Island. Bald eagles were the third most common cause of disturbance and were more frequent at Puffin Island than at other sites. In contrast with powerboats, sea kayaks were uncommon during the study and, therefore, caused fewer harassments (11% for all sites). Sea kayakers, however, were a greater potential disturbance to seals ashore than operators of powerboats. Fifty-five percent of kayakers (n=11) within 1 km of a haul-out site harassed harbor seals, whereas only 9% of powerboats (n=436) within 1 km caused harassment. This finding is a result of seals being less tolerant of kayaks and kayakers who generally travel closer to shore than do powerboaters.

Table 2

Percentage of harassments (n, excluding disturbances caused by bald eagles) that resulted in either full recovery, partial recovery, no recovery, or no chance to recover for harbor seals at Puffin Island, Clements Reef, and Skipjack Island, northern San Juan Islands, Washington, 1991 and 1992.

	Puffin Island (n=27)	Clements Reef (n=28)	Skipjack Island (n=11)
Full recovery	19%	54%	45%
Partial recovery	30%	32%	18%
No recovery	44%	7%	36%
No chance to recover	7%	7%	0
For all recoveries			
no. of harassments before low tide	10	11	5
no. of harrassments after low tide	17	17	6

The extent of recovery following harassments (excluding those caused by eagles) of harbor seals was less at Puffin Island than at Clements Reef and Skipjack Island (Table 2). Disturbances caused by eagles were excluded from this comparison because eagles were potential predators of pups (eagles were observed approaching and disturbing pups) and could affect recovery. Recovery was related to whether the harassment occurred before or after low tide (74% of full recoveries occurred before low tide, whereas 75% of partial and 89% of no recoveries occurred after low tide). This finding corresponds with total numbers of seals ashore typically decreasing one to two hours after low tide, independent of disturbance. For comparison of recovery among sites, the proportion of disturbances occurring before and after low tide was similar and likely did not influence results (Table 2).

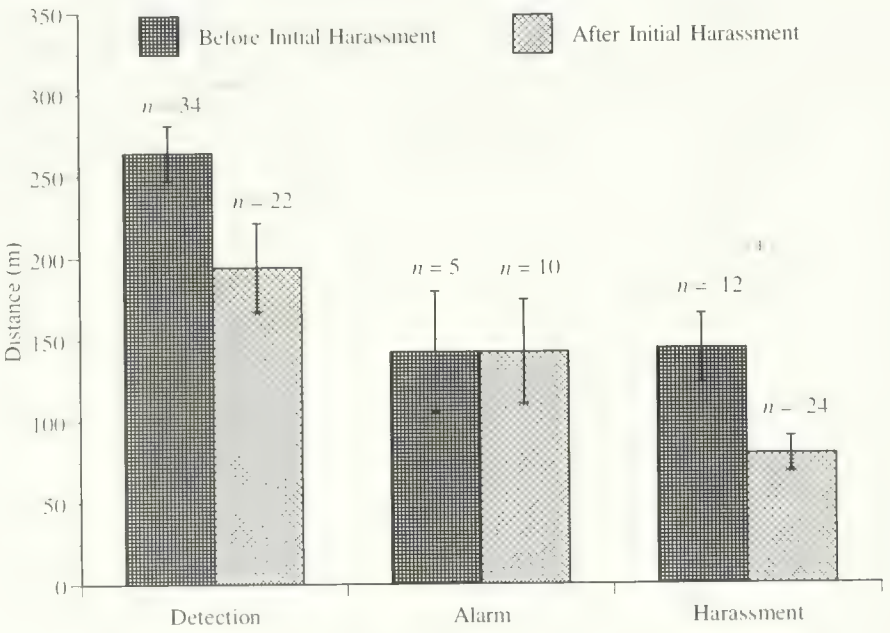

Figure 2

Mean distance (±SE) between harbor seals and powerboat for disturbances occurring before and after the initial harassment during a haul-out period. An asterisk (*) indicates a significant ($P<0.05$) difference between before and after initial harassment data for that disturbance category.

There was no apparent difference in the proportion of harbor seal pups onshore before and after harassments ($\chi^2=0.183$, $n=27$, $P>0.50$). Pups did not appear to be affected disproportionately to subadults and adults.

The percentage of vigilant harbor seals varied with each comparison (due to random subsampling of data to control for group size), hence there was no single value for percentage of vigilant harbor seals at each haul-out site. The percentage of vigilant harbor seals was significantly greater at Puffin Island compared with Clements Reef ($P=0.003$) and Skipjack Island ($P=0.002$; Table 3). This finding is likely due to the greater percentage of female-and-pup pairs at Puffin Island and, in addition to lower recovery, indicated seals were more susceptible to disturbance.

Powerboat speed did not significantly influence distance of disturbance. Lack of statistical significance was likely due to small sample sizes after subdividing data by approach speed and initial versus subsequent harassments. There was also no significant difference in distance of disturbance between sites (data were not collected at Skipjack Island). Given the large variability of the data and small effect size, greater than 450 observations would be required for a power of 0.80 to detect a significant difference between sites. Data, therefore, were pooled for further analysis. Twenty-five percent of harassments occurred when vessels were <100 m from seals, 50% occurred at 100–200 m, and 25% at 200–300 m. After detection by seals, powerboats were able to approach significantly closer ($F=10.51$, $P<0.001$) before causing alarm or harassment of seals (Fig. 2). Interestingly, we found that distances of initial disturbance were significantly greater than subsequent disturbances (Fig. 2). This indicated that seals remaining or returning to shore following the first harassment were less easily disturbed.

Discussion

Many islands in the San Juan Archipelago are state parks or have resort harbors that attract numerous boaters during the summer. Clements Reef is located near (0.6 km) Sucia Island, which is the most heavily visited state park in the northern islands. It was not surprising, therefore, that most disturbances at Clements Reef were caused by boaters. Relatively few kayakers ventured out to Clements Reef, Puffin Island, or Skipjack Island. Kayakers typically travel along the shoreline and have been shown to cause

Table 3

Mean percentage of vigilant harbor seals at Puffin Island versus Clements Reef and at Puffin Island versus Skipjack Island when no potential disturbance source was within 1 km of haul-out site. Two means (±SE) and separate statistical tests are presented for Puffin Island due to random subsampling to control for group size of each comparison.

	Mean (%)	SE	*n*	Mann-Whitney *U*	*P*
Puffin Island	4.43	0.44	17		
Clements Reef	2.41	0.47	17	*U*=229	0.003
Puffin Island	6.40	1.13	21		
Slipjack Island	2.46	0.75	21	*U*=343	0.002

harassment of harbor seals at a greater distance than do operators of powerboats (Calambokidis et al.[4]); therefore, as sea kayaking becomes more popular, there is a greater potential for disturbance of harbor seals ashore.

The differences in occurrence of unknown causes of disturbance among haul-out sites was possibly a result of haul-out site topography. Harbor seals on Clements Reef had a 360° view of potential sources of disturbance compared with roughly a 270° view for Puffin Island and 180° for Skipjack Island. A disturbance of unknown origin at Skipjack Island would often begin by several harbor seals looking toward the rocky cliff of the island, then entering the water. A high incidence of disturbances of unknown origin have also been documented at Gertrude Island (77%; Moss, 1992) and Protection Island (43%; Kroll, 1993), Washington. The relatively high occurrence of harassments by bald eagles at Puffin Island may have been due to a nearby bald eagle nest and the high percentage of harbor seal pups (immature eagles were observed harassing female and pup pairs). Skipjack Island also had an active bald eagle nest, but eagles were not observed harassing harbor seals.

Overall, only 39% of all harassments resulted in full recovery, indicating seals often remained in the water or moved to a different site. Allen et al. (1984) reported that the number of harbor seals that returned to a haul-out site after a disturbance in Bolinas Lagoon, California, was always less than the original number, and in most cases, harbor seals did not move to a nearby reef. Murphy and Hoover[3] reported that harbor seals off the Kenai fjords, Alaska, often searched for a new haul-out site after harassment. Disturbance to harbor seals, therefore, may have considerable impact where haul-out space is limited (Murphy and Hoover[3]). Although haul-out sites in the San Juan Islands are numerous, alternate sites for female and pup pairs, similar to Puffin Island, may not be readily accessible (particularly since there tended to be less recovery of seals at Puffin Island).

Terhune (1985) compared aggregation behavior and vigilance of harbor seals with flocking behavior of avian species—a behavior that allows individuals to decrease their surveillance without decreasing the probability of detecting a predator (Caraco, 1979; Studd et al., 1983). Da Silva and Terhune (1988) identified group size as the only factor accounting for variation in time taken to scan for predators. Renouf and Lawson (1986) suggested that only males increased scanning time as mating season approached, and scans were related to important events in their mating system, not predators. Results of our study indicated that increased vigilance may be related more to potential "predators" (loosely defined as any source of disturbance, human or animal). We found that seals at an area with a greater percentage of female-and-pup pairs scanned more frequently than those at other locations. Other researchers have described increased vigilance of females with pups. Stein (1989) reported female harbor seals rested alert significantly more frequently when their pups were one to nine days old than when pups were older. Newby (1973) reported a female harbor seal with a pup is "constantly alert and nervous."

The greater vigilance of harbor seals at Puffin Island than at Clements Reef and Skipjack Island and the lack of recovery from a harassment indicated that seals at a pupping location were affected more by disturbance. We therefore expected that seals at Puffin Island would enter the water when powerboats were farther away, in contrast with harbor seals at Clements Reef. This was not the case, there were no significant differences between sites. We cannot, however, conclude that seals at pupping locations tolerated boats to approach just as closely as seals at nonpupping sites without harassment because of differences in geographic characteristics of haul-out sites, unreplicated sites, and lack of power to detect a statistically significant difference.

Bishop (1967) observed that a nucleus of harbor seals, which usually included several very large animals, remained ashore unless danger became immi-

nent. Although we also observed certain groups of harbor seals (often small-size groups) entering the water well before others during a harassment, there was no significant trend. Terhune and Almon (1983) also noted that not all groups of harbor seals reacted to disturbances in the same manner.

The most notable difference in distance of disturbance was the decrease between initial and subsequent harassments. There are two plausible explanations for this: 1) seals became more tolerant of powerboat approaches; or 2) seals that were less tolerant of disturbance did not return to the haul-out site after the initial harassment. Based on lack of full recovery following initial harassments, our results support the latter possibility.

Allen et al. (1984) reported that boats advancing toward, or remaining near, harbor seals ashore at Bolinas Lagoon, California, caused seals to leave the haul-out site more often than a boat simply moving past seals. Boats that traveled slowly, parallel to the haul-out site, and made no abrupt move or changes in speed approached harbor seals at Clements Reef and Puffin Island with minimal disturbance. Greater sample sizes probably would have resulted in significant differences among distances of disturbance for various approach speeds and angles recorded during this study.

Additional potential factors affecting the distance at which seals were disturbed included time of day for haul-out period or location of haul-out site. Harbor seals may more readily enter the water toward the end of the haul-out period, if air temperature is high (Watts, 1992), or during rain. These considerations were not addressed in this study. Harbor seals also may become accustomed to close approaches (<15 m) by boats in areas of high boat traffic (authors' pers. obs.). In Woodard Bay, Calambokidis et al.[4] reported powerboats were able to approach to an average of 40 m before harbor seals entered the water. This area near Seattle, Washington, undoubtedly gets more year-around recreational traffic than the northern San Juan Islands which may explain why disturbance distances were over a third less than those observed during our study.

Most harassments in our study were caused by people approaching to view harbor seals. It is important therefore to distribute information and guidelines for wildlife viewing to the general public. An effective solution may be to include information with vessel registration.

Direct mortality of harbor seals or long-term abandonment of haul-out sites (greater than one haul-out period) because of harassment by humans was not observed during this study. Long-term impacts of harassment of harbor seal populations, however, are difficult to assess. Cases where marine mammals remain in heavily disturbed areas are easy to detect; therefore, cases of partial or complete abandonment of disturbed areas may be more common than evidence indicates (Richardson et al., 1995). Harassments increase energy expenditure of harbor seals by decreasing duration of haul-out period. Increased energy requirements likely have the greatest impact on harbor seal pups during nursing and on adult and subadult harbor seals during molt when access to haul-out sites is important. Brasseur et al. (1996), however, demonstrated that captive harbor seals may need to haul-out even outside these "critical" periods. Richardson et al. (1995) noted that occasional disturbance probably has little effect on harbor seal populations; repeated disturbance, however, may have significant negative effects especially at haul-out sites used for pup rearing.

Results of this study quantify the variability in response to disturbance among individuals and locations. We also demonstrated the potential bias in sampling animals that remain after an initial disturbance, or in areas of regular boat traffic. Distance at which powerboats caused harassment were variable, ranging from 28 m to 260 m. Boating regulations near harbor seal haul-out sites should address activity of vessel (speed and approach angle) in addition to distance from harbor seals. Boating precautions are particularly important near harbor seal pupping areas such as Puffin Island.

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Age, growth, longevity, and mortality of blackcheek tonguefish, *Symphurus plagiusa* (Cynoglossidae: Pleuronectiformes), in Chesapeake Bay, Virginia*

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Abstract.—Age structure, longevity, and mortality were determined for a population of blackcheek tonguefish, *Symphurus plagiusa*, in Chesapeake Bay. Blackcheek tonguefish (36–202 mm TL) were randomly collected by means of otter trawl in lower Chesapeake Bay and major Virginia tributaries (James, York, and Rappahannock rivers) from April 1994 through August 1995. Ages were determined by interpreting growth increments on thin transverse sections of sagittal otoliths. Marginal increment analysis showed that a single annulus was formed in June of each year. Blackcheek tonguefish caught during this study reached a maximum age of 5+ years. Growth was rapid during the first year, then slowed rapidly at a time coincident with maturation. We used the following von Bertalanffy growth equations: for males—$L_t = 196.5(1 - e^{-0.285(t + 0.92)})$; and for females—$L_t = 190.6(1 - e^{-0.320(t + 0.78)})$. Von Bertalanffy parameters were not significantly different between sexes. Extrapolated instantaneous mortality rates for a possible seventh year class were 0.73 (Hoenig's equation) and 0.77 (Royce's equation). High estimates of instantaneous total mortality may reflect either loss due to emigration of adults from Chesapeake Bay onto the continental shelf or high natural mortality occurring in this northernmost population. Compared with sympatric pleuronectiforms, blackcheek tonguefish have a relatively high mortality rate, small asymptotic length, and high growth parameter K. Species, such as blackcheek tonguefish, that feature this combination of growth parameters are hypothesized to be better adapted at exploiting seasonally dynamic and highly unpredictable environments, such as those estuarine habitats within Chesapeake Bay.

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The blackcheek tonguefish, *Symphurus plagiusa* (Linnaeus, 1766), ranges from Connecticut southward through the Florida Keys, northern Gulf of Mexico, Cuba, and the Bahamas (Ginsburg, 1951; Topp and Hoff, 1972; Munroe, 1998). Chesapeake Bay is the northernmost location of a major population of this species (Munroe, 1998). South of Chesapeake Bay, blackcheek tonguefishes are an abundant component of the fish fauna occurring in estuaries and inshore coastal waters. Within this region, they occur in sufficient numbers to form a minor component of the bycatch of demersal fisheries and also constitute a minor inclusion in landings reported for several industrial fisheries. In the shrimp trawl fishery, they are a potential nuisance because individuals frequently become embedded in the webbing of trawls to such an extent that they interfere with the gear's effectiveness (Topp and Hoff, 1972).

The blackcheek tonguefish is the only member of the pleuronectiform family Cynoglossidae occurring in Chesapeake Bay (Ginsburg, 1951; Murdy et al., 1997; Munroe, 1998). This species is among the top three most abundant pleuronectiforms occurring throughout lower Chesapeake Bay and its tributaries (Bonzek et al., 1993; Geer et al., 1997). Only the hogchoker, *Trinectes maculatus*, is commonly taken in greater abundance in bottom trawls made within the Bay. Occurrence of all life history stages in Chesapeake Bay (Olney and Grant, 1976; Terwilliger, 1996) suggests that blackcheek tonguefish is a resident species in this system.

Despite its abundance in different estuarine and nearshore marine habitats in the northwest Atlantic, life history parameters of *S. plagiusa* are largely unknown. Some previous works have described distribution, relative abundances and length frequencies for blackcheek tonguefish in South Carolina estuaries (Shealy et al., 1974); some have summarized size-related maturity patterns for individuals from throughout the entire range of the species (Munroe, 1998); some have

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investigated factors influencing recruitment (Miller et al., 1991); and some have described daily growth rates of juveniles in Georgia estuaries (Reichert and van der Veer, 1991). The minimal amount of published information on this species (summarized in Munroe, 1998) may be due in part to the relatively small size of the fish. It reaches a maximum size of approximately 210 mm total length (TL) (Wenner and Sedberry, 1989), but fish smaller than 165 mm TL are those most commonly taken in Chesapeake Bay by otter trawl (Terwilliger, 1996; Geer et al., 1997). Small size and benthic microinvertebrate feeding habits (Stickney, 1976; Reichert and van der Veer, 1991; Toepfer and Fleeger, 1995) render this species inaccessible to most recreational and commercial fishing gears used in Chesapeake Bay.

Few age and growth studies using bony structures or otoliths exist for species of the Cynoglossidae. This relatively large gap in knowledge for approximately 150 species of tonguefishes was recently noted in a compilation of flatfish life history parameters (Miller et al., 1991). Although several studies have described growth for species of *Cynoglossus* from the eastern Atlantic (Chauvet, 1972), western Pacific (Lin, 1982; Meng and Ren, 1988; Zhu and Ma, 1992), and Indian Ocean (Seshappa, 1976, 1978, 1981; Ramanathan et al., 1980; Seshappa and Chakrapani, 1984), no growth studies using bony structures or otoliths have been performed on species of *Symphurus*. Previous work describing the age structure of blackcheek tonguefish in Chesapeake Bay using length frequencies of fish taken by otter trawl (Bonzek et al., 1993) is limited because this type of analysis requires subjective interpretation of modal frequencies in the data, which, given the difficulty of distinguishing modal groups at older ages, renders the interpretation unreliable (Chauvet, 1972; White and Chittenden, 1977; Jearld, 1983; Barbieri, 1993). Such limitations in interpretation of age from length-frequency distributions are particularly evident in data from Koski's (1978) study on hogchokers from the Hudson River estuary, where the first of bimodal peaks in a frequency distribution of hogchoker lengths corresponded to age-1 fish, whereas the second peak represented combinations of length distributions for fishes age 2–6 yr. Chauvet's (1972) data for *C. canariensis* off West Africa also show a similar pattern of overlapping sizes among fishes of different ages.

Symphurus plagiusa is a good candidate for an age and growth study. It is unique among the Cynoglossidae in that it is the only species of this family that inhabits estuarine environments in the seasonally dynamic region of north temperate latitudes. Most other cynoglossid species occur in the tropics and are difficult to age from hard parts because environmental constancy precludes the formation of interpretable annular growth marks on these structures (Qasim, 1973). Other species of symphurine tonguefishes that occur in temperate waters generally are small-size, deep-water forms that are difficult to catch in abundance (Munroe, 1998).

This study was undertaken to determine age structure, growth rate, longevity, and mortality for a population of *S. plagiusa* residing in Chesapeake Bay, Virginia. Knowledge about life history parameters for this species provides a window of understanding into the biology of the Cynoglossidae, as well as insights into age, growth, and longevity of other small-size, estuarine-dependent flatfishes.

Materials and methods

Blackcheek tonguefishes were collected by 9.14-m semiballoon otter trawl with a 38.10-mm stretch mesh body, 6.35-mm mesh codend liner, and attached tickler chain (Bonzek et al., 1993). Fish were collected from April 1994 through August 1995 during the Virginia Institute of Marine Science (VIMS) Juvenile Finfish and Blue Crab Stock Assessment Program's trawl survey. The survey employs a monthly, random-stratified design of the lower Chesapeake Bay and fixed-station mid-channel transects in each of three major Virginia tributaries: the York, James, and Rappahannock rivers (Fig. 1). Details of sampling design were provided in Geer et al. (1993).

Samples of blackcheek tonguefishes selected from trawl catches were brought to the laboratory, measured for total length (TL) to the nearest millimeter and for total weight (TW) taken to the nearest hundredth of a gram. When samples were small, all fish were used in age analyses; however, fish were randomly selected for age analyses from relatively large samples. Regressions were fitted to the length–weight data, and regressions on log-transformed data for male and female blackcheek tonguefish were compared by using analysis of covariance (ANCOVA). The formula to convert SL to TL for blackcheek tonguefish provided by Jorgenson and Miller (1968:11) was used when comparing length data (reported as SL) from other studies.

All fish were sexed macroscopically, and then gonads were removed and preserved for later histological analysis to determine maturity stages (Terwilliger, 1996). Males were classified as either immature or mature according to the absence or presence of spermatozoa in the testes; females were considered mature if they showed any evidence of developing oocytes or previous spawning, e.g. thickening of the ovarian membrane.

Both sagittal otoliths were removed, cleaned, and stored dry for later processing. Otolith maximum

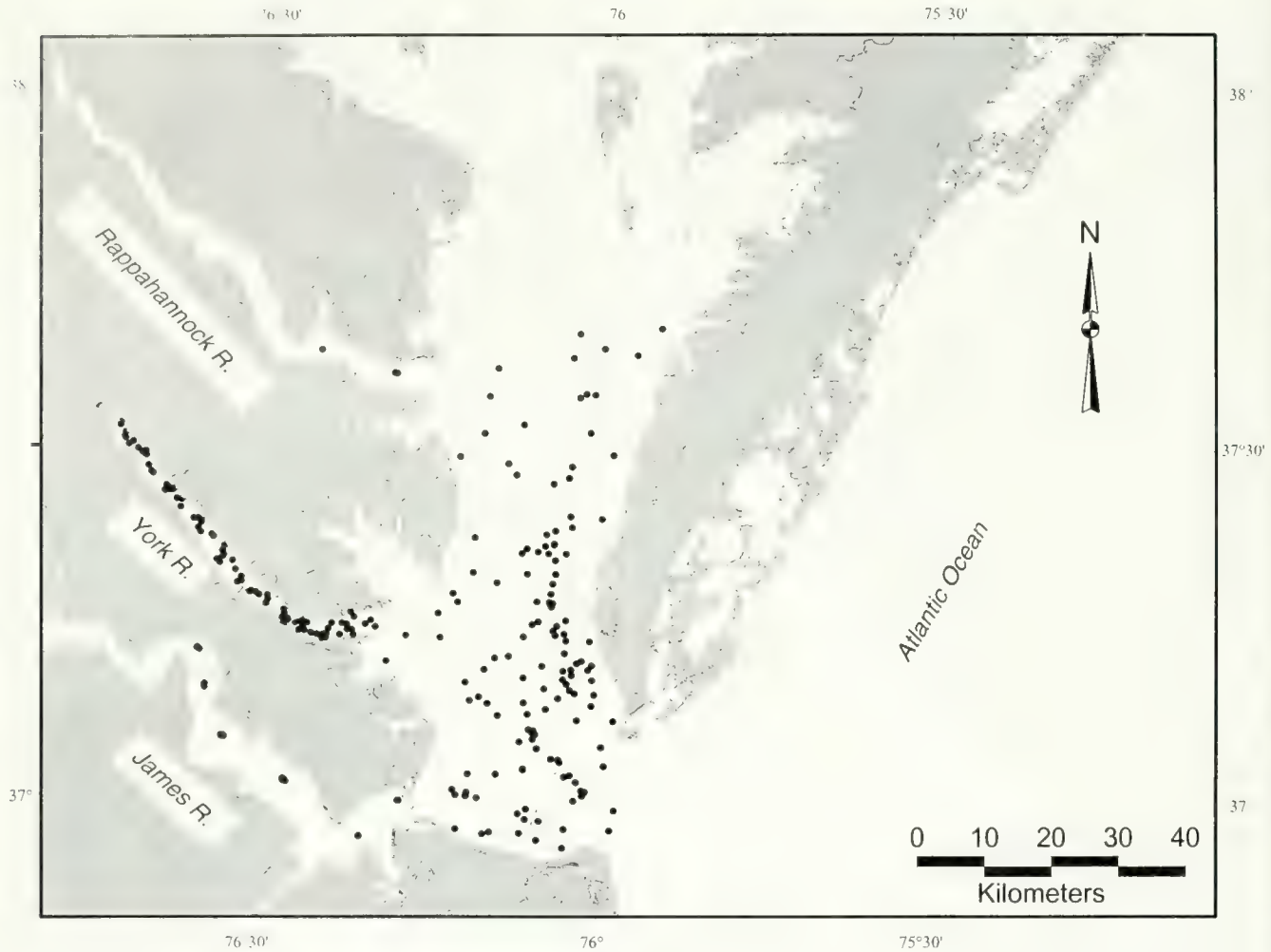

Figure 1

Lower Chesapeake Bay system, including James, York, and Rappahannock rivers. Points indicate stations where blackcheek tonguefish, *Symphurus plagiusa*, were collected, April 1994–August 1995.

diameter (distance from anterior tip of rostrum to postrostrum) was measured to the nearest 0.00001 mm by using a compound microscope coupled with a video camera interfaced with a microcomputer equipped with Biosonics' Optical Pattern Recognition System (OPRS) software (Biosonics, Inc., 1987). Because no asymmetry in otolith shape was apparent, sagittal otoliths (left or right) were arbitrarily selected from each fish for age analysis, embedded in epoxy resin (Spurr, 1969), and sectioned transversely (1 mm thick) through the core with a Buehler Isomet low-speed saw with duel diamond blades. Sections were mounted on glass slides with Crystal Bond adhesive, sanded with 1000-grit sandpaper to remove saw marks and to gain proximity to the core, polished with alumina powder, and examined with a binocular dissecting microscope (30×) with transmitted light and bright field. Annuli on otoliths from all 566 blackcheek tonguefish were counted once a month for three months. Counts were made without information regarding fish length or catch date. In 185 (32.7%) cases, the first and second readings did not agree and a third reading was made. The majority of disagreements in age estimates occurred during the beginning of the study; subsequent re-ageing resolved most discrepancies in age estimates. In most cases, the second reading of an otolith section differed from the first reading by only one year. If a third reading agreed with either of the first two, then that age was assigned to the otolith. In 28 (5%) cases, the third reading was different than the first and second readings. These 28 otoliths were considered unreadable and excluded from further analysis.

Otolith annuli were validated by the marginal increment method (Bagenal and Tesch, 1978; Jearld, 1983). Distances from the core to each annulus and the proximal edge were computed by drawing a vertical line from the core to the proximal edge of the

otolith with the OPRS. The average margin width, i.e. the translucent region between the last annulus and the proximal edge of the otolith, was plotted by month.

Regression analyses of otolith maximum diameter on total length and of weight on total length were calculated by the method of least squares. Back-calculated lengths-at-age were computed by using the Lee method (Lagler, 1956). To evaluate growth, back-calculated lengths-at-ages were fitted to the von Bertalanffy model (Ricker, 1975) by using nonlinear regression (Marquardt method) calculated with Fishparm computer software (Saila et al., 1988). Likelihood-ratio tests were used to compare parameter estimates of the von Bertalanffy equation for males and females (Kimura, 1980; Cerrato, 1990).

A scale sample from a region in the posterior third of the body, dorsal to the midline, was taken from all fish. Six scales from each fish were cleaned with hydrogen peroxide and mounted on plastic strips by using a Carver hydraulic laboratory press. A random sample of scale strips from 50 fish were then viewed with a microfiche reader in order to discern annuli for comparison with otolith sections. In contrast to otoliths, scales proved to be unreliable for ageing this species. Annuli were poorly defined and difficult to distinguish, and in many cases, the scales were unreadable. Fish ages obtained from scales agreed with ages obtained from otoliths in only 12% of the cases. This is not surprising, because scale annuli from other fish species with known ages have been shown to be inconsistent indicators of age, even in relatively young fish (Prather, 1967; Heidinger and Clodfelter, 1987).

Instantaneous total annual mortality rates, Z, were estimated from maximum age estimates with a pooled regression equation as suggested by Hoenig (1983) and by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972) as described in Chittenden and McEachran (1976). Values of Z were converted to total annual mortality rates, A, using the relationship $A = 1 - e^{-Z}$ (Ricker, 1975).

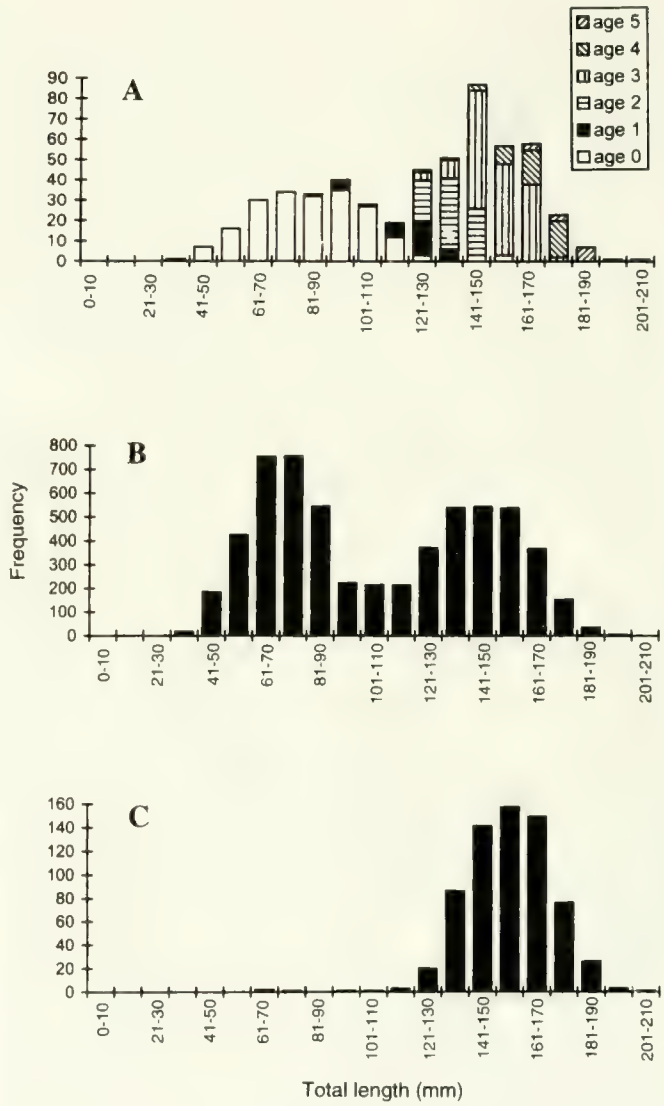

Figure 2

Length-frequency distribution for blackcheek tonguefish, *Symphurus plagiusa*: (**A**) length frequency for blackcheek tonguefish from lower Chesapeake Bay and major lower tributaries for fishes aged in this study; (**B**) length frequency for blackcheek tonguefish caught by Virginia Institute of Marine Science's juvenile fish recruitment trawl survey in lower Chesapeake Bay and major lower tributaries, 1993–1996; (**C**) length frequency for blackcheek tonguefish caught at the mouth of Chesapeake Bay and inner shelf off Virginia and North Carolina, 1987–89.

Results

A total of 566 fish, encompassing a size range from 36 to 202 mm TL (Fig. 2A), were used in this ageing study. This size range included individuals from all life history stages from postsettling juveniles to mature adults. The sex ratio for blackcheek tonguefish collected in this study was 223 males:343 females, or 1:1.54. A G-test of the sex ratio for 566 blackcheek tonguefish indicated statistically significant deviations (G=25.64; df=1; P<0.001) from a 1:1 sex ratio (Table 1). A G-test of sex ratios for blackcheek

Table 1

G-test of sex ratio for blackcheek tonguefish, *Symphurus plagiusa*, caught in lower Chesapeake Bay and three Virginia tributaries, April 1994–August 1995 (**A**) total catch; (**B**) by 25 mm size increment. Yates' correction for continuity implemented in (**B**) due to small sample sizes. *n* = number of fish; df = degrees of freedom; ns = nonsignificant.

A

	Males	Females	*n*	df	*G*	*P*
Frequency	223	343	566	1	25.64	10.83*
Expected	283	283				

* $P<0.001$.

B

Length	Males	Females	*n*	df	*G*	*P*
26–50	7.5	4.5	12	1	0.7580146	ns
Expected	6.0	6.0				
51–75	18.5	36.5	55	1	6.0008514	5.024**
Expected	27.5	27.5				
76–100	46.5	53.5	100	1	0.4904009	ns
Expected	50.0	50.0				
101–125	26.5	44.5	71	1	4.6135656	3.841*
Expected	35.5	35.5				
126–150	68.5	106.5	175	1	8.3175269	7.879***
Expected	87.5	87.5				
151–175	51.5	91.5	143	1	11.339487	10.828****
Expected	71.5	71.5				
176–200	7.5	8.5	16	1	0.0625408	ns
Expected	8.0	8.0				
201–225	0.5	1.5	2	1	0.5232481	ns
Expected	1.0	1.0				

$P<0.05$, $P<0.025$, $P<0.005$, *** $P<0.001$

tonguefish broken down into 25-mm length increments showed that females dominated many intermediate size classes (Table 1).

The length–weight relationships for 200 males (48–190 mm TL) and 310 females (46–202 mm TL) (Fig. 3) were

$$\text{Males:} \quad W = 10^{-5.30}(TL^{3.126}),$$
$$\text{Females:} \quad W = 10^{-5.37}(TL^{3.163}).$$

No statistically significant differences were found between sexes in the total length-total weight relationships (ANCOVA; F=3.86; df=506; P>0.25). The length-weight relationship for sexes combined was

$$W = 10^{-5.34}(TL^{3.145}).$$

Size at sexual maturity observed in female and male blackcheek tonguefish ranged between 80–130 mm TL and 70–110 mm TL, respectively. Length at which 50% of the population reached maturity was 101 mm TL for females and 91 mm TL for males (Fig. 4).

Sagittal otoliths of blackcheek tonguefish are small, round, dense structures that cannot be read whole. Transverse sections of otoliths (Fig. 5), however, revealed fairly distinct opaque bands that could be counted. Transverse sections through otoliths indicated that otolith structure consists of an opaque core usually surrounded by a wide opaque area whose outer edge demarcates the first annulus. Size and appearance of this first annulus vary among fish, ranging from a broad band continuous with the core to a narrow opaque band not continuous with the core. Subsequent annuli are represented by thin opaque bands encircling the core and by broader translucent zones found between annuli. At the margin of the otolith, an annulus was difficult to observe. However, when sufficient spring and early summer growth had occurred and contributed translucent material to the margin of the otolith after annulus

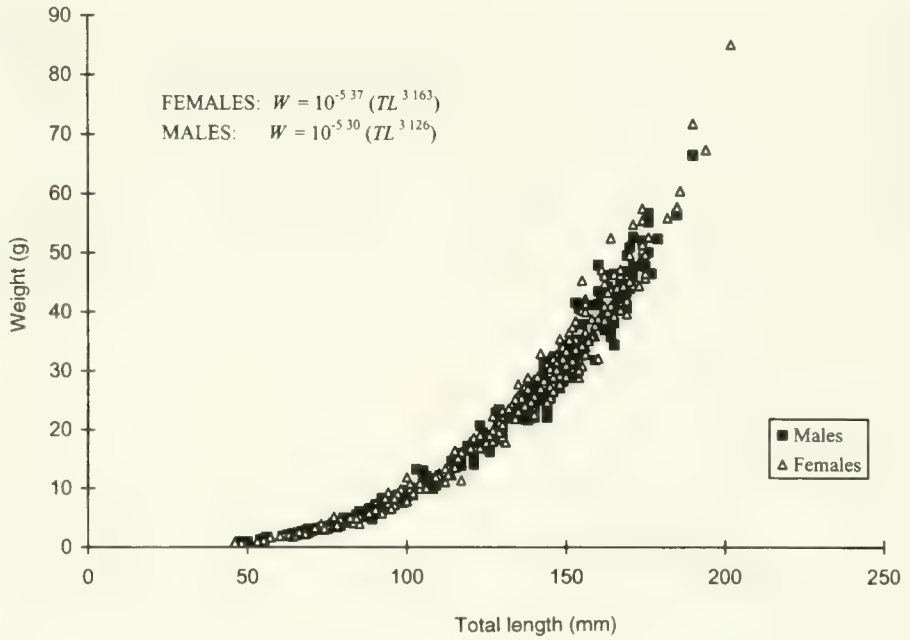

Figure 3

Total length–weight relationship for both sexes of blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

formation, the densely compacted opaque zone delimiting the annulus was easily identifiable. The combination of one broad translucent zone and one narrow opaque zone (Fig. 5) represents one year's growth.

Otolith maximum diameter (OMD) was linearly related to total length (Fig. 6) and described by the following relationship:

$$TL = 64.59(OMD) - 17.02. \qquad [r^2=0.93]$$

This linear relationship indicated that otolith growth was proportional to fish growth.

Size at first annulus formation for blackcheek tonguefish ranged from 88 to 138 mm TL (mean length ca. 118 mm TL). Seasonal progression of modal length frequencies (Fig. 7) for young-of-the-year fish (YOY) corroborated first-year growth-rate estimates determined from annular marks on the otoliths. Pooled data for 1993–96 from VIMS[1] trawl survey reports indicated that YOY blackcheek tonguefish recruited to the gear during September, usually at sizes of ca. 35–45 mm TL. By the following June, these fish had reached sizes ranging from ca. 53 to 138 mm TL. Thus, empirical data from length frequencies agreed fairly well with first-year growth estimates derived from interpretation of annulus formation on the otoliths.

Monthly mean marginal increments on the otoliths were plotted for fish from all age groups (Fig. 8). The seasonal progression of marginal increments was similar on otoliths from all age groups; therefore, data were pooled to demonstrate general trends in annual growth. Marginal increments were smallest during June of both 1994 and 1995. Monthly mean marginal increments showed only one trough during a year, indicating that a single annulus is formed yearly in June. In 1994, margin width on the otoliths increased rapidly during July and August, reflecting an active period of growth. After August 1994, margin width leveled off and remained fairly constant from September 1994 through May 1995. Large variation (indicated by high standard error) for samples taken during May of both 1994 and 1995 may indicate that the season of annulus formation may be somewhat more protracted (May–June) and perhaps dependent upon environmental factors. Alternatively, it may simply reflect an artifact of the small sample sizes examined from this period.

Mean lengths at age were backcalculated for 92 males and 145 females (Table 2). Remaining fish were young-of-the-year and therefore were excluded from this analysis. Observed (empirical) lengths were con-

[1] VIMS (Virginia Institute of Marine Science), Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

sistently higher than the back-calculated lengths-at-age for individual age groups, which indicated that seasonal growth had occurred since formation of a new annulus. Differences between back-calculated lengths-at-age and observed lengths are in the range of observed seasonal growth. Males and females have similar lengths-at-age until age 4 (Table 2). Beyond age 4, mean lengths for females were slightly greater than those for males. The largest male collected in this study was 190 mm (age 5+); the largest female collected was 202 mm (age 5+).

Greatest incremental growth in TL for both sexes occurred during the first year and then declined rapidly thereafter (Table 2). Mean back-calculated lengths for females and males at the end of their first year were 78.84 mm and 75.68 mm, respectively. Growth for both sexes in the second year was only 39–41% of that recorded for the first year. Growth increments continued to decrease every year thereafter for both sexes until age 5, when the estimated growth increment increased slightly for both sexes. This increase at age 5 may be an artifact due to the relatively small number of samples for both sexes in this age group.

Length frequency for blackcheek tonguefish caught by VIMS[2] trawl survey (1993–96) shows a bimodal distribution (Fig. 2B), but this distribution does not adequately reflect age composition of the individuals, especially for fishes larger than 110 mm TL. Despite the bimodal distribution in length frequencies, six age groups are represented in this distribution, and much overlap in total length exists between age groups, especially those consisting of medium- and large-size fish. These data indicate that length frequency analyses are unreliable age estimators for older individuals of this species.

Von Bertalanffy parameters were computed (Table 3) by using lengths backcalculated to the most recent annuli to reduce bias in asymptotic length and growth coefficient K due to the presence of Lee's phenomenon in the back-calculated lengths-at-age (Vaughan and Burton, 1994). The growth coefficient K for female blackcheek tonguefishes (0.320) was greater than that (0.285) calculated for males. Males and females achieved 50% of L_∞ by the end of their first year and 75% between ages 2 and 3 (Fig. 9). Results of likelihood-ratio tests (Table 4) showed no significant differences in the overall von Bertalanffy growth models for males and females (χ^2=6.56, df=3, P=0.09). Estimates of L_∞ (χ^2=0.10, df=1, P=0.75), K (χ^2=0.03, df=1, P=0.87), and t_0 (χ^2=0.19, df=1, P=0.67) were not significantly different between sexes.

Values for asymptotic lengths for both sexes agreed well with observed lengths. The largest male collected in this study was 190 mm and the calculated L_∞ for males was 196.5 mm. The largest female collected in this study was 202 mm and the calculated asymptotic length for females was 190.6 mm. These results are acceptable because asymptotic length is a regression estimate, and thus an average that represents an average maximum length if fish live and grow according to the von Bertalanffy equation. Nevertheless, the overall estimated asymptotic length value (192.4) represents a reasonable approximation of the average maximum length estimate for the species.

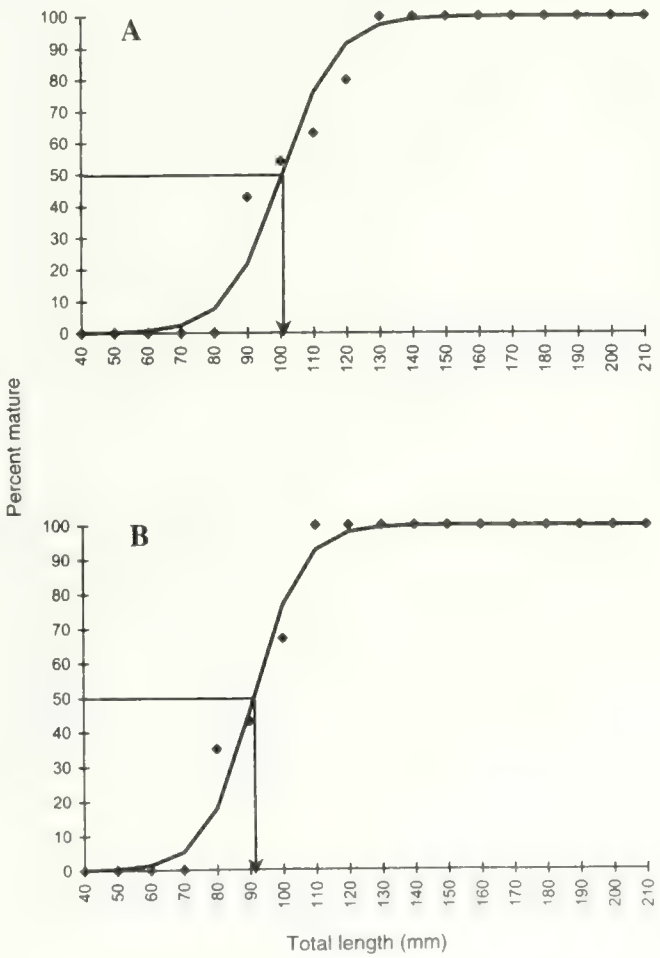

Figure 4

Length at maturity for blackcheek tonguefish, *Symphurus plagiusa*, in lower Chesapeake Bay and major lower tributaries: (**A**) females; (**B**) males. Arrow represents length at 50% maturity.

[2] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

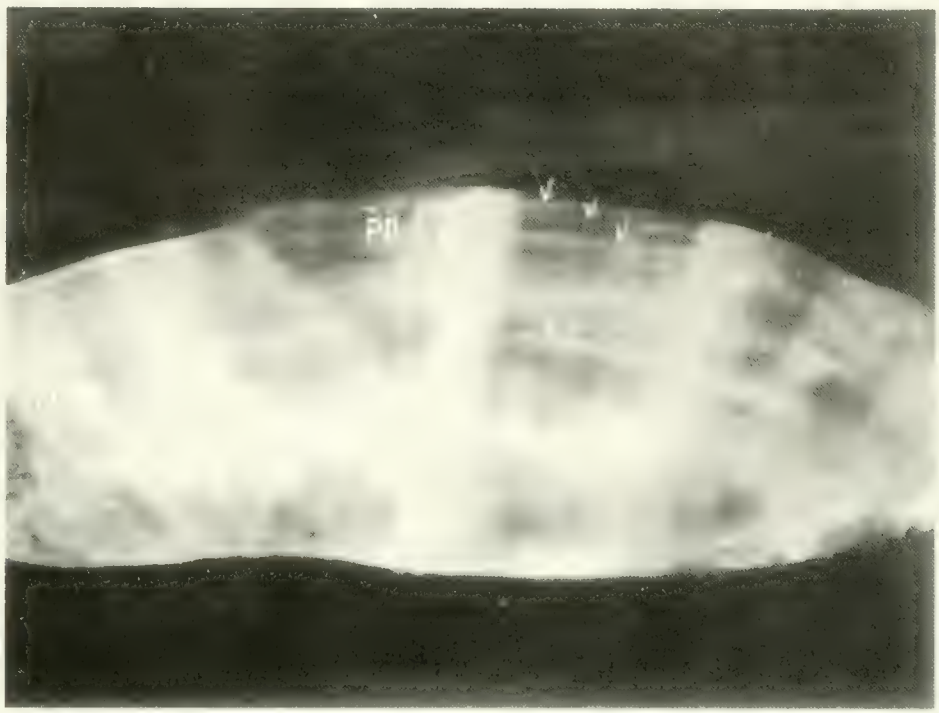

Figure 5

Transverse section from a sagittal otolith of a blackcheek tonguefish, *Symphurus plagiusa*, collected in lower Chesapeake Bay and major lower tributaries. Age 5+. Arrows indicate annuli. Pr = proximal; Ro = rostral.

Table 2

Mean observed and back-calculated lengths for female and male blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay: ages 1–5.

Age	Sample size	Size range (mm)	Mean observed length (mm)	Mean back-calculated lengths at successive annuli (mm)				
				I	II	III	IV	V
Females								
1	15	93–138	121.07	83.943				
2	31	127–155	136.81	81.156	115.272			
3	64	126–170	153.33	76.038	113.238	135.832		
4	25	135–175	161.62	70.073	101.826	126.549	145.385	
5	10	162–202	181.20	82.966	108.644	129.812	150.714	167.936
Mean length				78.835	109.745	130.731	148.049	167.936
Growth increment				78.835	30.910	20.986	17.318	19.887
Males								
1	12	88–125	115.83	81.778				
2	22	103–146	136.59	82.844	113.864			
3	31	130–171	154.19	76.573	110.408	133.553		
4	23	146–179	166.52	73.339	107.662	129.228	148.911	
5	4	162–190	177.75	63.838	95.125	118.058	141.277	163.721
Mean length				75.675	106.765	126.946	145.094	163.721
Growth increment				75.675	31.090	20.182	18.147	18.628

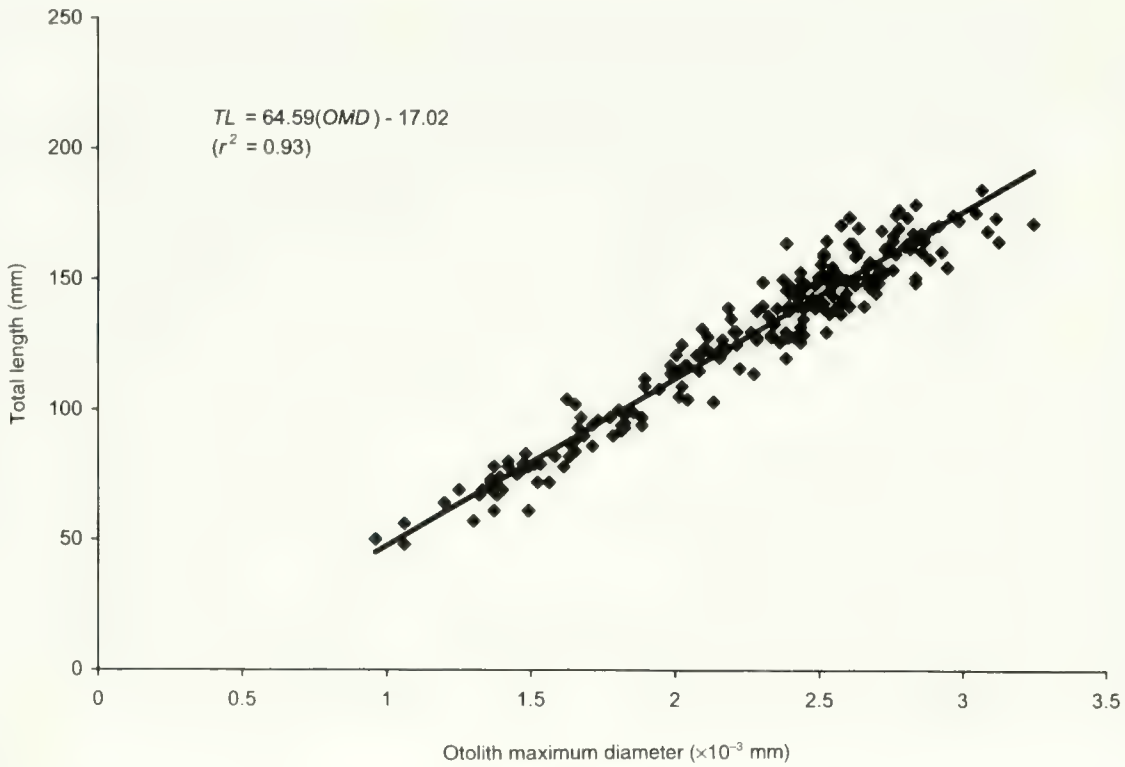

Figure 6

Linear regression of total length (mm) on otolith maximum diameter (mm) for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries.

Instantaneous total mortality (Z) estimates obtained for a maximum age of 5 years were 0.87 (A=58%) with Hoenig's (1983) method, and 0.92 (A=60%) with Royce's (1972) method. A plot of age composition of the catch (Fig. 10) indicates rapidly declining numbers of fishes aged 4 and 5.

Discussion

Most of what we know regarding growth in cynoglossid flatfishes stems from information gathered from studies conducted on species of *Cynoglossus*. These are tonguefishes usually much larger in size than species of *Symphurus* (Menon, 1977), and species which also occur predominantly in the shallow tropical seas of the Indo-West Pacific. Therefore, the present study detailing information on age, growth, and longevity for blackcheek tonguefish is significant in being the first of its kind reporting such life history parameters for a member of *Symphurus*. Furthermore, of the approximately 150 species of Cynoglossidae, *S. plagiusa* is unique in that it is the only member of the family inhabiting temperate estuarine environments in the seasonally dynamic Chesapeake Bay region of the western North Atlantic. In fact, the tonguefishes inhabiting Chesapeake Bay are the northernmost major population of this species (Munroe, 1998). Here, the species has ranked as high as sixth in overall abundance, and in some years is the second most abundant pleuronectiform among fishes taken during trawling in lower Chesapeake Bay and its tributaries (Geer et al., 1993). North of the Chesapeake Bay region, adult blackcheek tonguefish are relatively rare (Munroe, 1998), even in such proximate estuaries as Delaware Bay. Just how long the Chesapeake Bay has supported a significant population of this species is unknown because earlier compilations on fishes of the region (Hildebrand and Schroeder, 1928) regarded this species as occurring only rarely within the Bay. It is conceivable that because of its relatively small size and benthic habits, the abundance of this species may have been grossly underestimated during previous fish surveys conducted in this region. However, given the general rarity of this species in areas immediately to the north, and the observed incidences of winter mortalities within Chesapeake Bay (see be-

Table 3

Von Bertalanffy parameters and equations calculated for male and female blackcheek tonguefish, *Symphurus plagiusa*, collected in Chesapeake Bay, Virginia. Values in parentheses are standard errors.

Parameter	Males	Females	Combined
K	0.285	0.320	0.308
	(0.075)	(0.061)	(0.047)
L_∞	196.5	190.6	192.4
	(20.04)	(13.03)	(10.88)
t_0	–0.920	–0.784	–0.832
	(0.289)	(0.216)	(0.172)
Equation	$L_t = 196.5\ (1 - e^{-0.285(t + 0.920)})$	$L_t = 190.6\ (1 - e^{-0.320(t + 0.784)})$	$L_t = 192.4\ (1 - e^{-0.308(t + 0.832)})$

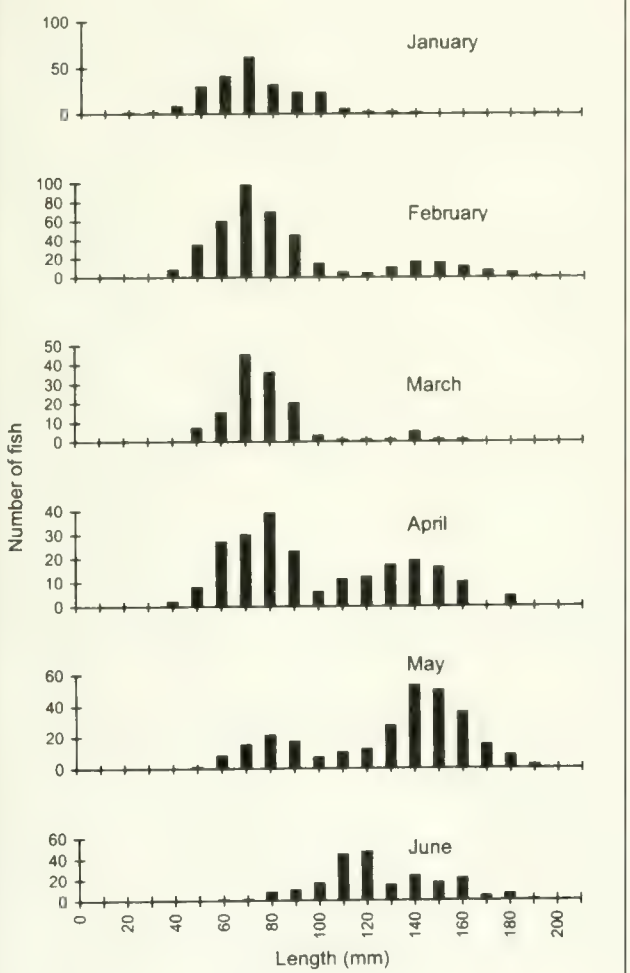

Figure 7

Seasonal progression of modal length frequencies for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries, 1993–96.

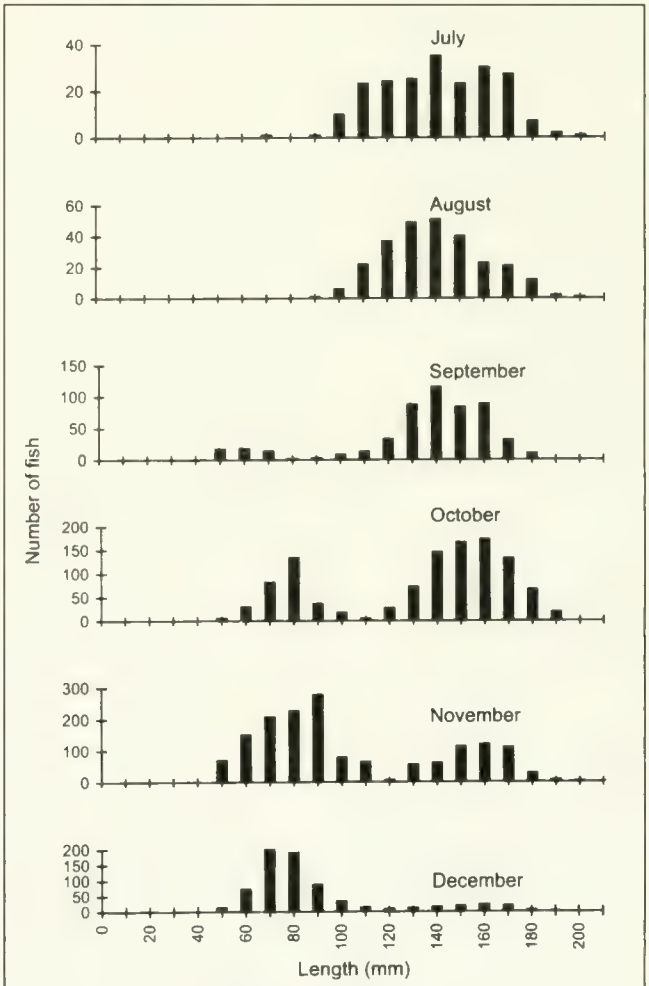

Figure 7 (continued)

low), it also seems equally possible that the population of blackcheek tonguefishes residing in Chesapeake Bay could be of more recent origin because all other major populations for this species are known to occur only in areas further to the south. If indeed this is the case, then life history parameters estimated for blackcheek tonguefishes from Chesapeake Bay are those characterizing a peripheral population of the species. Comparisons of these estimates

of life history parameters, then, with values derived from other, more centrally located, populations of this species, as well as with those from populations inhabiting subtropical environments in northern Mexico and Cuba (Munroe, 1998), would prove interesting from the perspective of discovering the range of variability in life history features that has evolved within this species of flatfish.

Sizes of blackcheek tonguefishes collected within Chesapeake Bay during the present study represent almost the complete size range known for the species (Munroe, 1998). The largest female (202 mm TL) and largest male (190 mm TL) taken within the Bay approach the largest sizes known for this species (ca. 210 mm TL; Wenner and Sedberry, 1989). However, most blackcheek tonguefishes occurring within this system were smaller, with total lengths usually ranging between 35 and 150 mm. The size range for blackcheek tonguefishes occurring in Chesapeake Bay is not unlike those reported for other estuarine populations located throughout the species' range. For example, Shealy et al. (1974) reported that, during a year-long survey of fish assemblages in South Carolina estuaries, blackcheek tonguefishes ranged in size from 53 to 156 mm TL. However, modal lengths for this species were never greater than 140 mm TL, and fish were usually much smaller (monthly mean size 97–124 mm TL). In fact, of the blackcheek tonguefishes taken during that study, only 8 of 362 (2.2%) were 150 mm TL or larger.

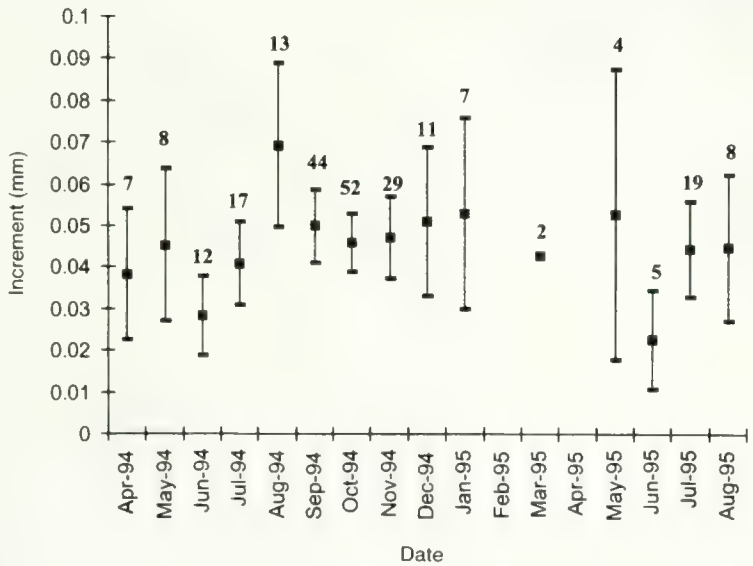

Figure 8

Plot of monthly mean marginal increments for blackcheek tonguefish, *Symphurus plagiusa*, ages 1–5, collected in lower Chesapeake Bay and major lower tributaries. Vertical bars represent ±1 standard error. Numbers above bars represent monthly sample sizes.

Although many studies (summarized in Munroe, 1998) have reported catching large blackcheek tonguefish from neritic habitats on the inner continental shelf throughout the species' range, size ranges for these fishes were not unlike those observed for blackcheek tonguefishes collected within Chesapeake Bay. For example, blackcheek tonguefishes (n=439) collected at the mouth of Chesapeake Bay and on the inner continental shelf off southern Virginia and northern North Carolina (VIMS[3]) during a series of cruises conducted during 1987–89 ranged from 68 to 203 mm TL (mean size= 154.5 mm TL; Fig. 2C); and most fishes

[3] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

Table 4

Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) blackcheek tonguefish, *Symphurus plagiusa*, from Chesapeake Bay, Virginia. df = degrees of freedom.

Hypothesis	Linear constraints	Residual SS	χ^2_r	df	P
HΩ	none	99,760.5			
Hω1	$L_{\infty 1} = L_{\infty 2}$	99,780.9	0.1043	1	0.7467
Hω2	$K_1 = K_2$	99,765.8	0.0271	1	0.8692
Hω3	$t_{01} = t_{02}$	99,796.9	0.1861	1	0.6661
Hω4	$L_{\infty 1} = L_{\infty 2}$	10,051.6	6.558	3	0.0874
	$K_1 = K_2$				
	$t_{01} = t_{02}$				

measured 140–180 mm TL. Lengths of fishes collected within the Bay system completely overlap those taken from the nearby shelf. Munroe (1998) noted that most blackcheek tonguefishes in collections from throughout the species' geographic range were usually much smaller than the largest sizes known for the species because only 4% of 568 fish he examined exceeded 164 mm TL. Wenner and Sedberry (1989) sampled 8780 blackcheek tonguefishes from coastal habitats (<10 m depth) between Cape Fear, North Carolina, and the St. Johns River, Florida, and reported that length composition of trawl-caught *S. plagiusa* was consistent from season to season, with mean sizes ranging between 140–150 mm TL. The largest specimens taken during that study were 210 mm TL, and few fish <100 mm TL were caught, possibly because fish smaller than this inhabited a different habitat as juveniles or because they did not recruit to the fishing gear until 100 mm TL. On the continental shelf off Tampa Bay, Florida, lengths (124–174 mm TL) for blackcheek tonguefishes were also similar to those reported for fish from Chesapeake Bay (Moe and Martin, 1965).

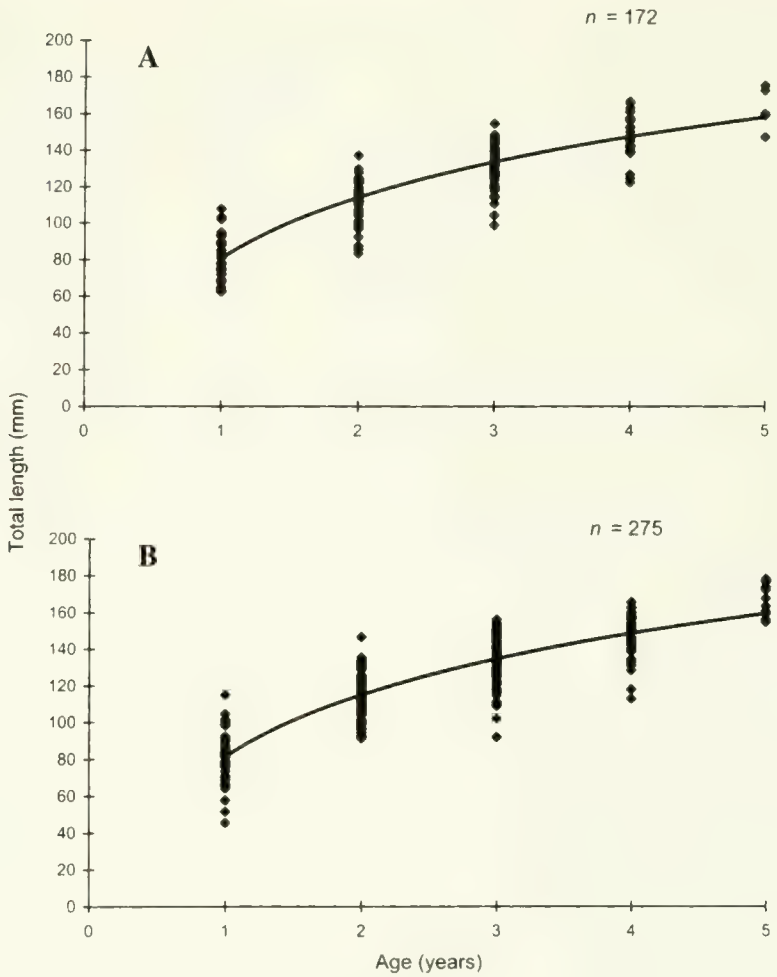

Figure 9

Plot of back-calculated and predicted lengths from the von Bertalanffy growth model for blackcheek tonguefish, *Symphurus plagiusa*, from lower Chesapeake Bay and major lower tributaries: (**A**) males; (**B**) females.

Although age estimates are not available for other populations of blackcheek tonguefish, a general comparison of growth between blackcheek tonguefishes occurring in Chesapeake Bay with those from other areas is provided by examination of length–weight parameters derived for different populations. Dawson (1965) generated a length-weight relationship for 3504 blackcheek tonguefish (43–148 mm TL) occurring in Gulf of Mexico waters. With this relationship, weights were generated from 510 randomly selected lengths between 43 and 148 mm TL and these were then compared with a similar number of weights generated for fishes of the same size range by using the length-weight relationship derived for blackcheek tonguefishes from Chesapeake Bay. No significant differences (t=0.53; df=1010; P=0.60) were evident in this comparison between weights of fishes of these two regions, indicating that growth in weight, at least, is similar for fishes of this size range occurring in these widely separated areas within the species' range.

Annuli form on the otoliths of blackcheek tonguefishes from late spring through early summer (mostly June), coincident with the summer warming period and also at the initiation of the spawning season (Terwilliger, 1996). For *C. abbreviatus*, a tonguefish occurring in temperate seas off eastern China (Zhu and Ma, 1992), annuli form on otoliths during March–May, a period also corresponding to seasonal timing of gonad maturation and warming of water temperatures. Koski (1978) reported that annuli form on scales of hogchokers in the Hudson River from April to mid-June, which is a period of increasing water temperature, and for mature fish this also corresponds to the time just prior to and overlapping the early spawning season.

Flatfishes typically exhibit sexual dimorphism in size at age (Roff, 1982; and others, see below)—

females usually growing larger than males. In the Chesapeake Bay population, male and female blackcheek tonguefishes attain similar maximum sizes (mean value for oldest females=181.2 mm TL; mean value for oldest males=177.8 mm TL). In summarizing size information for blackcheek tonguefishes collected throughout the geographic range of the species, Munroe (1998) also reported no significant size differences between males (to 174 mm TL) and females (to 172 mm TL). For 23 other species of western Atlantic tonguefishes, females reached larger sizes than males in 11 of these species, in six others a larger size was reported for males, whereas in seven other species similar maximum sizes were attained by both sexes (Munroe, 1998). However, since no age estimates have been made for these other species of *Symphurus*, comparative data on dimorphism in lengths at age for these symphurine tonguefishes are unavailable. For other cynoglossids with accompanying age data, considerable variation exists in the degree of sexual dimorphism evident in sizes attained by the sexes. In the Malabar sole (*Cynoglossus semifasciatus*) off India, females grow larger than males, although reported differences in maximum sizes between sexes were relatively small (Seshappa and Bhimacher, 1954). Similarly, although female *C. abbreviatus* (to 348 mm TL) from Jiaozhua Bay, China, were larger than males (to 321 mm TL), average total lengths at age between the sexes were not significantly different (Zhu and Ma, 1992). Females of *C. bilineatus* and *C. arel* were also reported to be larger than males sampled from the same populations (Hoda and Khalil, 1995), whereas sizes for adult female (83–173 mm TL) and male (84–168 mm TL) *C. macrostomus* were found to be similar (Victor, 1981). Female *C. canariensis* also grow larger than males (Chauvet, 1972). For *C. semilaevis* inhabiting the Bohai Sea, China (Meng and Ren, 1988), quite a different situation exists. In this species, females attain lengths (to 638 mm TL) slightly more than twice those reached by males (to 312 mm TL). In other estuarine flatfish, such as the hogchoker, which occurs throughout much of the geographic range of the blackcheek tonguefish, females grow to larger sizes than do males from the same population (Koski, 1978). For most species of the Pleuronectidae, females also typically grow larger and have both a later age and larger size at maturity than do males (Cooper[4]).

Back-calculated lengths-at-age for blackcheek tonguefishes were consistently less than observed lengths-at-age for all age groups combined, which may be attributed to Lee's phenomenon. The principal cause of Lee's phenomenon in unexploited fish populations, such as that of blackcheek tonguefish inhabiting Chesapeake Bay, is that faster growing fish tend to mature and die earlier than do smaller members of the same year class (Gerking, 1957; Ricker, 1975). When a larger proportion of older fish die, the result is a smaller estimated size for fish at younger ages than the true average size at the age in question. Since blackcheek tonguefishes are not harvested commercially or recreationally within the Bay, the presence of Lee's phenomenon in the back-calculation estimates may be due to higher mortality of larger individuals within an age class, or possibly this finding may reflect the fact that larger fish move out of the Bay system and onto the nearby shelf region. The ages of blackcheek tonguefishes occurring on the continental shelf throughout the species' range are unknown. No offshore samples of blackcheek tonguefishes were collected during this study, and it is unknown if any of these fish are older than those occurring in Chesapeake Bay.

Although female blackcheek tonguefishes captured in Chesapeake Bay grew at a slightly faster rate than did males, observed differences in back-calculated lengths between male and female blackcheek tonguefishes beyond age 4 were not statistically significantly different. However, our sample sizes for older fish were small and interpretation of data for this oldest age class is limited. In other cynoglossids, such as Malabar sole, faster growth has also been observed in females compared with that for males (Seshappa and Bhimachar, 1954). Rajaguru (1992) found that female *C. arel* grew faster than males, but no significant differences in growth patterns were found between female and male *C. lida*. After their first year, female hogchokers in the Hudson River also grew faster than males (Koski, 1978). In some species of the Soleidae, such as the Agulhas sole (*Austroglossus pectoralis*) occurring off South Africa (Zoutendyk, 1974) and *Solea solea* in Spanish waters (Ramos, 1982), females also have a faster growth rate than do males within the same populations. A faster growth rate for females compared with that of males has also been reported in a variety of other flatfish species (Chen et al., 1992; Santos, 1994).

Estimates of the growth parameter K (Table 5) for blackcheek tonguefish are relatively high, indicating that these fish reach their asymptotic length relatively rapidly (Francis, 1996). Few estimates of K-values are available for other tonguefishes, but for those species studied, growth rates are relatively high. Where data are available, all, except two species, have higher growth coefficients reported for females. In *C. arel*, K-values were 0.315 for females and 0.238 for males, and in *C. lida* K-values of 0.233

[4] Cooper, J. A. 1998. National Marine Fisheries Service, National Systematics Laboratory, Washington, DC 20560. Personal commun.

for females and 0.223 for males were reported (Rajaguru, 1992). For *C. abbreviatus* (Zhu and Ma, 1992), *K*-values were 0.395 for females and 0.344 for males. In two of the largest species in the family, *C. semilaevis* and *C. canariensis*, the estimated *K*-values were higher for males compared with those for females. In *C. semilaevis*, *K*-value for females was 0.264, and that of males was 0.352 (Meng and Ren, 1988). For female *C. senegalensis* the *K*-value was 0.32 compared with 0.36 for males (Chauvet, 1972).

In Chesapeake Bay, blackcheek tonguefishes achieve most of their growth in length during their first year. Males and females attained up to 50% of their total growth in length by the end of their first year, and up to 72% of their total growth by the end of their second year. Such rapid first-year growth does not appear to be unusual among members of the Cynoglossidae. For example, male *C. arel* grew between 180–194 mm TL, and females from 201–210 mm TL, during their first year (Rajaguru, 1992), which represented up to 58% and 51% of their total growth in length (333 and 393 mm, respectively). Similar to the pattern observed in blackcheek tonguefish, second-year growth in this species was estimated to be only 18% and 21% of the total growth, respectively, for males and females. In *C. lida*, males (151–154 mm TL) and females (153–156 mm TL) also reached fairly large sizes during their first year of life, with first-year growth for males and females ranging between 69 and 71% of the total growth in length (216 and 218 mm, respectively), compared with second-year growth values of only 13–14% of the total length (Rajaguru, 1992). *Cynoglossus macrolepidotus* also has a high growth rate during its first year, reaching a length of about 160 mm TL, and like the preceding species, during the second and subsequent years there occurs a marked reduction (only 10–30 mm increase/yr) in growth rate (Kutty, 1967). Likewise, in *C. abbreviatus* (Zhu and Ma, 1992), first-year growth is maximal for both sexes (males to 162 mm TL, females to 178 mm TL; representing 50% and 51% of total growth, respectively), whereas second-year growth in this species averages only about 16% or less of the total growth. This growth pattern was also apparent for *C. canariensis* where male and female fish, respectively, achieved 50% and 55% of their total growth in length during the first year, compared with second-year growth equalling only 14–15% of the total growth in length (Chauvet, 1972). In another large-size species, *C. semilaevis*, first-year growth is also rapid, with males reaching 141 mm TL at end of year one and females growing to 194 mm TL, values that represent 45% and 30% of the total growth in length achieved by this species (Meng and Ren, 1988). However, in contrast to other cynoglossid species examined thus far, growth in this species during the second year differs markedly between the sexes. For females, the average growth increment during the second year was greater than that of the first year (to 307 mm TL, 36% of total growth in length), whereas during this same time interval males averaged only about one-half of the growth increment attained during year one (to 204 mm TL, representing 20% of total growth). In the hogchoker, growth in length is also rapid; males and females achieve 56% and 44% of their total growth in length during the first year (Koski, 1978). By the end of their second year, hogchokers have reached on average 74% (males) and 63% (females) of their total growth in length.

The substantial reduction in growth rate beyond age 1 noted for blackcheek tonguefishes occurs at a time coincident with maturation (Terwilliger, 1996). Roff (1982) noted that, for fish in general, it is frequently observed that rate of growth decreases with

Table 5

Comparision of von Bertalanffy parameters of selected Pleuronectiformes occuring in temperate estuaries of the western North Atlantic.

Species	Parameters	Source
Paralichthys dentatus (♂♀)	K: 0.215 L_∞: 859 mm t_0: –0.690	Desfosse, 1995
Paralichthys lethostigma (♀)	K: 0.235 L_∞: 760 mm t_0: 0.570	Miller et al., 1991
Scophthalmus aquosus (♂)	K: 0.272 L_∞: 383 mm t_0: 0.418	Miller et al., 1991
Pseudopleuronectes americanus (♀)	K: 0.217 L_∞: 375.8 mm t_0: 0.730	Miller et al., 1991
Symphurus plagiusa (♀♂)	K: 0.308 L_∞: 192.4 mm t_0: –0.832	Terwilliger, 1996
Trinectes maculatus (♀)	K: 0.195 L_∞: 209.5 mm t_0: –0.353	Miller et al., 1991

the onset of maturity. This slowing in somatic growth may reflect an allocation of energy to gonadal development, or may be a response to other physiological processes associated with maturation. Other cynoglossid species that have been aged also mature sexually at a relatively early age even in some of the larger-size species. Seshappa and Bhimachar (1954) reported that young Malabar soles (*C. semifasciatus*) grew to adult size within a year or less and that after maturation, growth slowed distinctly. After an initially high growth rate during their first year, there also occurred a marked reduction in the growth rate of *C. macrolepidotus* during their second year, at a time coincident with initiation of the spawning season (Kutty, 1967). Likewise, in other cynoglossids (*C. arel* and *C. lida*) occurring off India, growth during the first year is also rapid and this fast growth period is then followed by a considerable reduction in the growth rate during the next year when the fishes matured sexually (Rajaguru, 1992). In *C. arel*, for example, which reaches total lengths to 333 mm SL, males and females mature at sizes of about 217 mm TL and 225 mm TL, respectively, sizes reached by this species at the beginning of their second year of life. In *C. lida*, size at 50% maturity is 167 mm TL for males, and 179 mm TL for females. These represent sizes that are reached by the fish during the beginning of their second year of life. For *C. dubius* (Seshappa, 1976) minimum size at maturity was reported to be about 287 mm TL for females, a size that corresponded to fish approximately 2–3 years old. In *C. canariensis*, a species reaching total lengths of 486 mm (males) and 519 mm (females), maturity occurs at about 1.5 years when fish are about 300 mm TL (Chauvet, 1972).

Hoenig's and Royce's mortality estimates, based on the maximum known age of a species, indicate a relatively high instantaneous total mortality in the blackcheek tonguefish population inhabiting Chesapeake Bay (Table 6). Relatively few of the blackcheek tonguefishes within Chesapeake Bay are older than three years. The age structure observed in this population may, however, reflect the relatively short life span of this species (5+ years), or it could also reflect high mortality levels experienced by blackcheek tonguefishes in the Bay environment; undoubtedly it would also be influenced by the emigration of larger individuals from the Bay system.

Relatively short life spans may be typical of species of *Symphurus* and of the Cynoglossidae, in general. In fact, some dwarf species of tropical *Symphurus* reach maximum sizes of only 35–45 mm SL (Munroe, 1990, 1998) and probably live no more than a year. Age estimates based on growth marks interpreted from scales of tonguefishes occurring in coastal waters off India indicate that Malabar sole reach an age of only about 2+ years (Seshappa and Bhimachar, 1954). Based on studies of tonguefishes from the west coast of India, a life span of 3–4 years was reported by Seshappa (1978, 1981) for *C. lida* (size to 220 mm TL; most 140–189 mm TL) and *C. puncticeps* (to 209 mm TL; most 90–179 mm TL), whereas a life span of 6+ years (to 339 mm TL; most 160–299 mm TL) was reported for *C. bilineatus* from the same region. More recently, Rajaguru (1992) reported that *C. arel* and *C. lida* along the southeast coast of India have life spans just over 3 years. For *C. dubius* off India (to 414 mm TL), age estimates were 6+ years for most individuals, although some individuals reached 10 years (Seshappa, 1976). *Cynoglossus arel* off Taiwan (Lin, 1982) live to be at least 4 years. Kutty (1967) reported a maximum age of 6–7 years for *C. macrolepidotus* (to 330 mm TL). For *C. canariensis* (to 519 mm TL) off tropical West Africa, both sexes live to at least 8 years (Chauvet, 1972). For the temperate species, *C. abbreviatus*, from Jiaozhua Bay, China (Zhu and Ma, 1992), which is commercially exploited, females reach 8 years and males live to 7 years, and total mortality for this population was estimated to be very high (0.607). For

Table 6

Mortality estimates (Z) for various northwestern Atlantic Pleuronectiformes based on Hoenig's and Royce's equations. Values in parentheses reflect extrapolated mortality rates for a possible seventh age class of blackcheek tonguefish, *Symphurus plagiusa*, found in lower Chesapeake Bay and the inner continental shelf.

Species	Maximum age	Hoenig's equation	Royce's equation	Data source
Winter flounder (*P. americanus*)	14 years	0.32	0.33	Lux, 1973
Summer flounder (*P. dentatus*)	9 years	0.49	0.51	Desfosse, 1995
Windowpane (*S. aquosus*)	7 years	0.62	0.66	Moore, 1947
Southern flounder (*P. lethostigma*)	6 years	0.73	0.77	Music and Pafford, 1984
Hogchoker (*T. maculatus*)	6 years	0.73	0.77	Mansuetti and Pauly, 1956
Blackcheek tonguefish (*S. plagiusa*)	5 years (6 years)	0.87 (0.73)	0.92 (0.77)	Terwilliger, 1996

C. semilaevis from Chinese waters, a strong sexual dichotomy in longevity was apparent in the population studied; females reached 14 years (most 2–8 years), whereas males in this population attained a maximum age of only 5 years (Meng and Ren, 1988). By comparison, longevity estimates for a variety of other flatfishes occurring in temperate latitudes and from families other than the Cynoglossidae range from 6 to 30 years (Devold, 1942; Arora, 1951; Pitt, 1967; Lux and Nichy, 1969; Lux, 1970, 1973; Koski, 1978; Wada, 1970; Zoutendyk, 1974; Smith and Daiber, 1977).

As stated earlier, the population of *S. plagiusa* in Chesapeake Bay represents the northernmost location of a major population of this species (Munroe, 1998). In the western North Atlantic, variability in abiotic conditions increases from southern to northern latitudes (Parr, 1933; Miller et al., 1991). Abiotic variability also increases in environments located closer to the shoreline (Russell-Hunter, 1970; Miller et al., 1991). Fluctuations in abiotic factors, especially seasonal extremes of temperature during winter, may contribute to the high level of total instantaneous mortality measured for blackcheek tonguefishes within Chesapeake Bay. Bottom trawls conducted in this system during late winter and early spring of some years (1996, for example) catch numerous dead and moribund tonguefishes (Geer[5]), apparently due to stresses associated with extremely cold water temperatures (ca. 2°C. in 1996). More extreme winter temperatures and longer duration of cold temperatures may be a factor limiting the establishment of populations of blackcheek tonguefishes in more northern estuaries, where this species is known only by the occurrence of newly settled juveniles. In coastal estuaries throughout its U.S. geographic range, blackcheek tonguefishes appear to be sensitive to extreme winter temperatures, because winter mortalities have also been reported for this species in estuaries even as far south as those in Texas (McEachron et al., 1994). In addition to causing death outright, stresses associated with extreme winter temperatures may also render weakened tonguefishes easier prey to predators and thus further contribute to winter mortalities.

Mortality estimates for the population of blackcheek tonguefishes residing in Chesapeake Bay may also be inflated due to emigration of larger individuals out of the Bay and onto the nearby continental shelf. Hildebrand and Cable (1930) earlier had suggested that adult blackcheek tonguefishes in North Carolina estuaries undergo a seaward migration during May–August. An autumn emigration of blackcheek tonguefishes from Chesapeake Bay to the nearby shelf region just outside of the Bay may be reflected in the significantly larger catches (mean no./tow) of blackcheek tonguefishes reported (VIMS[6]) in this region during fall sampling (1987, 75.4/tow; 1988, 25.7/tow) compared with springtime catches (1987, 11.0/tow; 1988, 4.37/tow; 1989, 2.2/tow). Data supplied in Wenner and Sedberry (1989) also support the hypothesis that there is a seasonal migration of larger tonguefishes out of estuaries and onto the coastal shelf off South Carolina. They reported that this species was widespread throughout the survey area but noted that significant seasonal differences were apparent in the frequency of occurrence and abundance of *S. plagiusa* in coastal habitats. This species occurred less frequently during winter (48% of all tows; 566 individuals) than in spring (85% of tows; 1,460 individuals), summer (76% of tows; 798 individuals), or fall (94% of tows; 5962 individuals). Catches (mean no./tow) of this species were lowest in summer (8/tow) and winter (9/tow), higher in spring (21/tow), and highest during the fall (62/tow), when the largest fish (up to 210 mm TL) were taken. Although Wenner and Sedberry (and other studies) have reported that it is usually only larger-size blackcheek tonguefishes that are captured on the inner shelf region, no studies have verified any seasonal or spawning movements of blackcheek tonguefishes out of the estuaries, or the amount of exchange of individuals within populations between estuarine embayments and adjacent neritic habitats on the inner shelf. It is also unknown whether all larger individuals undergo an ontogenetic migration out of estuaries onto the nearby shelf; what portion of a population residing in estuaries moves out onto the shelf at any given age; what the estuarine residency time is for larger tonguefishes, especially in such larger and deeper estuaries as the Chesapeake Bay which may be utilized by larger tonguefishes for longer periods of time; or even if further exchange of individuals between these two environments occurs once an individual has emigrated beyond the estuarine boundary. Analysis of catch curve data (Fig. 10) may also lend insight on inflated mortality estimates. Although the bimodality of the catch curve data infers possible variability in year-class strength that invalidates its use for mortality estimations (Robson and Chapman, 1961; Everhart and Youngs, 1981), the data suggest that a seventh year class may exist, possibly on the nearby shelf region. If so, mortality estimates based on a maximum age of 5+ years

[5] Geer, P. J. 1996. VIMS, Department of Fisheries, Gloucester Point, VA 23062. Personal commun.

[6] VIMS, Department of Fisheries, Gloucester Point, VA 23062. Unpubl. data.

would be inflated compared with those calculated for an older year class.

Sex ratio of tonguefishes sampled during this study deviated from 1:1 mostly due to large single-sex catches of females during the summer months in the lower Bay. In lower Chesapeake Bay, apparently some spatial separation of the sexes occurs (Terwilliger, 1996). Here, dense concentrations of female blackcheek tonguefishes were commonly found in the deeper areas, and fewer males were taken in the same trawls. Among sympatric species of pleuronectiforms, the hogchoker also reportedly displays bathymetric separation of the sexes in tributaries of Chesapeake Bay during the summer months prior to spawning (Mansuetti and Pauly, 1956), when females occupy grass beds and shoal regions, while males are surmised to occupy deeper areas within the estuary. This pattern of habitat segregation by adult hogchokers, however, was not evident in the study conducted by Koski (1978) in the Hudson River, although he noted that although the overall sex ratio for fishes examined did not differ from 1:1, some individual trawl catches were dominated by or consisted entirely of one sex. Significant differences in the sex ratios of catches of other tonguefishes have also been reported. Seshappa and Bhimachar (1955) noted that sex ratios of catches of Malabar sole during the spawning period were markedly different than those made during other times of the year and attributed these differences to differential behavior of the two sexes during their spawning migrations. Hoda and Khalil (1995) also reported skewed sex ratios (1.0:2.55 males to females) for catches of *Cynoglossus arel*, whereas those (1.16:1) for *C. bilineatus* were not significantly different from 1:1. A skewed ratio (1.56:1) favoring females over males was also found for *C. semilaevis* (Meng and Ren, 1988). Although some studies have inferred spatial differences in movements of the different sexes of cynoglossid tonguefishes based on fisheries catch data, it is difficult to draw any general conclusions from these data. Just as we lack reliable documentation concerning spatial movements for the two sexes of blackcheek tonguefish, directed studies providing the detailed information necessary for interpreting adult movements of any of these other cynoglossid species have yet to be performed.

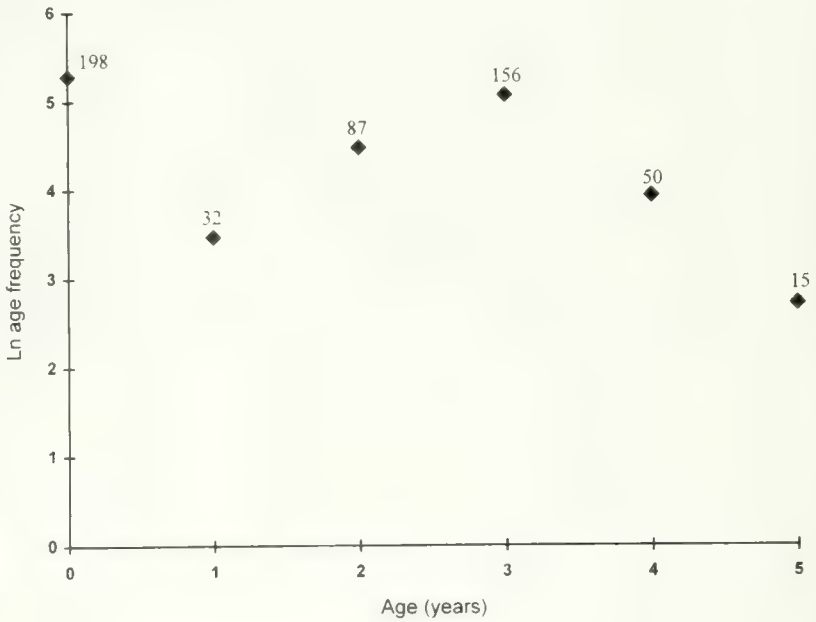

Figure 10

Catch curve for blackcheek tonguefish, *Symphurus plagiusa*, collected by otter trawl in lower Chesapeake Bay and major lower tributaries, 1993–95. Numbers above plot represent numbers at each age.

North temperate estuaries, such as Chesapeake Bay, are rigorous physical systems well known for environmental extremes in temperature, salinity, and dissolved oxygen, and for strong seasonal cycles of primary and secondary production. However, the extensive distribution within the Bay and its tributaries of shallow, soft bottom sediments presents considerable amounts of suitable habitat for flatfishes. Twelve species of flatfishes have been recorded from the Bay (Murdy et al., 1997). The unique geographical location of Chesapeake Bay at the northern end of a warm temperate and southern end of a cold temperate region (Briggs, 1974) may account for the occurrence within the Bay of diverse faunal components, which have either warm or cold water affinities. Among pleuronectiforms inhabiting Chesapeake Bay, for example, are six species representing five different families (Cynoglossidae, Achiridae, Paralichthyidae, Scophthalmidae, and Pleuronectidae). This assemblage includes representatives of families whose species occur primarily in cold temperate or boreal areas (Scophthalmidae, Pleuronectidae) or in warm temperate and tropical regions (Cynoglossidae, Achiridae, Paralichthyidae). Of the species occurring within Chesapeake Bay are blackcheek tonguefish, hogchoker, and smallmouth flounder,

Etropus microstomus (to ca. 159 mm TL), small-size species that are not commercially or recreationally exploited and ones that complete their life cycles within the Bay. Virtually nothing is known concerning age and growth of smallmouth flounder, especially within the Bay system; therefore further comparisons of its life history with those of sympatric flatfishes are limited. The flatfish fauna of the Bay also includes summer flounder (*Paralichthys dentatus*), southern flounder (*Paralichthys lethostigma*), windowpane (*Scophthalmus aquosus*), and winter flounder (*Pseudopleuronectes americanus*), species that do not necessarily complete their life cycles entirely within Chesapeake Bay and ones that are heavily exploited both commercially and recreationally. The remaining species of flatfishes recorded from the Bay are transient species that occur only irregularly within the Bay and will not be discussed further. The diversity in size and growth parameters represented among those flatfishes occurring in Chesapeake Bay which have been studied provides an interesting opportunity for investigating comparative life histories of sympatric members of an estuarine benthic fish assemblage with somewhat similar lifestyles (Table 5).

Few published age-growth studies exist for noncommercially exploited flatfishes, especially for those species occurring in temperate estuaries of the western North Atlantic. Von Bertalanffy growth parameters for species other than blackcheek tonguefish were taken from data found in the literature (Miller et al., 1991; Desfosse, 1995). These data reveal that among this assemblage, blackcheek tonguefish have the highest value for growth parameter K (Table 5), and therefore reach asymptotic length faster than sympatric counterparts (Francis, 1996). Of sympatric flatfishes occurring in Chesapeake Bay, only hogchokers display growth parameters and maturation schedules (some males mature at end of first year, most of both sexes mature by age 2; Koski, 1978) similar to those observed for blackcheek tonguefish. In contrast, summer and southern flounders mature at ages 2–3, windowpane flounders mature at ages 3 or 4, and winter flounders mature at ages 2–5. Later age at maturation in these species reflects a different life history pattern, and one that allows for energy allocation favoring increased somatic growth during several years prior to the onset of maturation. Because these other species mature at later ages than do blackcheek tonguefish and hogchoker, growth in length for these fishes would be relatively rapid over the course of several years during the early part of their lives (Fig. 11).

Estimates of asymptotic length, reflecting average maximum length attained by a species, also varies considerably among members of this assemblage. Asymptotic lengths for summer flounder (859 mm TL) and southern flounder (to 760 mm) greatly exceed those for blackcheek tonguefish and hogchoker (192 and 210 mm, respectively). In fact, these fishes grow more during their first year than do blackcheek tonguefish and hogchokers in a lifetime. Windowpane and winter flounder (383 and 376 mm, respectively) attain asymptotic lengths intermediate to these other two groups of sympatrically occurring estuarine flatfishes.

Estimates of instantaneous total mortality based on blackcheek tonguefishes caught within Chesapeake Bay during this study are also relatively higher when compared with those for most other estuarine dependent species of northwestern Atlantic Pleuronectiformes (Table 6). In this comparison, blackcheek tonguefish are among the shortest-lived species and therefore have one of the higher rates of instantaneous total mortality. Relatively few individuals within Chesapeake Bay are older than three years. Extrapolating mortality rates for a possible seventh year class (age 6+), which may be found on the inner shelf region, provides an instantaneous total mortality estimate comparable to those for hogchokers and southern flounder caught in Chesapeake Bay.

Blackcheek tonguefish exhibit the youngest age at first maturity, the highest growth coefficient, the youngest known maximum age, and the smallest asymptotic length when compared with sympatric pleuronectiforms from Chesapeake Bay. Blackcheek tonguefish exhibit rapid growth until maturity, after which growth rate declines markedly. Munroe (1990, 1998) indicated that eight dwarf species of *Symphurus* reach sexual maturity between 28 and 45 mm SL. Small size and presumably early age at maturation may be characteristic of species in this genus (Munroe, 1988); even *S. jenynsi*, the largest species in the genus (reaching ca. 350 mm TL), matures at a relatively small size (about 132 mm TL). More ageing studies on fishes of this genus are required to test this hypothesis. Other cynoglossid flatfishes, although they attain a relatively large size before reaching sexual maturity, are only 1 or 2 yr old when first maturing. According to available data, it is quite possible then that tonguefishes in general have an age dependent maturity schedule. Roff (1982) indicated that age, and not size, would appear to be most important in fish species that mature early. Data for tonguefishes support that finding.

When compared with estimates for sympatric flatfishes, blackcheek tonguefish caught during this study exhibit the highest rates of instantaneous total mortality. Other species inhabiting the Bay system also mature at larger sizes, have larger asymptotic lengths, and slower growth rates. Interesting

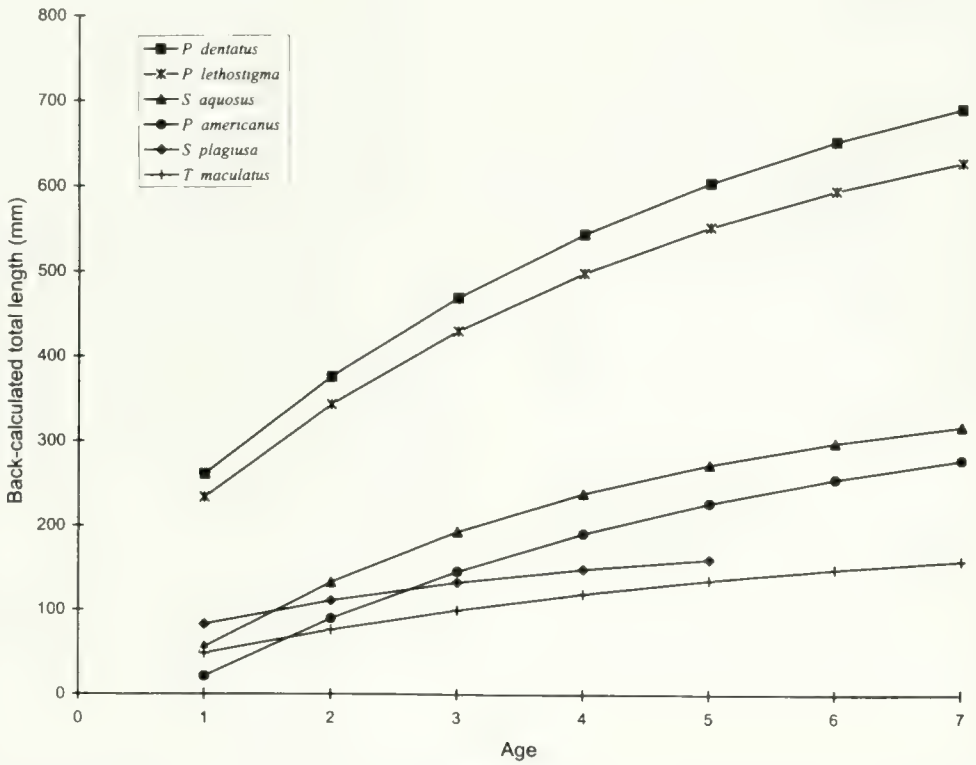

Figure 11

Von Bertalanffy growth curves for selected Pleuronectiformes occurring in western North Atlantic temperate estuaries. Values for species other than *Symphurus plagiusa* were derived from the literature.

to note, it is only the smallest-size and shortest-lived flatfishes (*S. plagiusa, T. maculatus*, and probably *E. microstomus*) that complete their life cycles within Chesapeake Bay. Under an environmental regime with a large component of unpredictable, nonselective mortality, an organism is hypothesized to allocate a larger portion of its resources to reproductive activities (Adams, 1980). Life history parameters, such as rapid growth, small body size, early age at maturity and relatively short life span, characteristics featured in these small-size flatfishes completing their life cycles within Chesapeake Bay, are consistent with those observed for other fish species that survive in and successfully exploit seasonally dynamic and highly unpredictable environments.

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Age distribution and growth of greater amberjack, *Seriola dumerili*, from the north-central Gulf of Mexico*

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Abstract.—The lack of age and growth estimates and population parameters for the amberjack family prompted our study to describe otolith structure and determine size-at-age and growth rates of greater amberjack (*Seriola dumerili*) from the north-central Gulf of Mexico.

Greater amberjack age and growth was described from a combination of external ridges and internal annuli in sectioned sagittal otoliths. A mark-recapture study using tetracycline was consistent with a single annulus being formed each year in two- and three-year-old amberjack. Tag-recapture data from the Gulf of Mexico and South Atlantic Cooperative Gamefish Tagging Program also confirmed that a single annulus increment was formed each year. Ages for 597 specimens ranged from young-of-the-year to 15 years, and all fish over 9 years were female. Sagittal weight provided a reliable estimation of fork length with a relationship of $FL = 151(1 - e^{-0.04 SW+1.6})$; a negative exponential equation in the form of the von Bertalanffy equation. The fit of the negative exponential in this application provides evidence of the disassociation between otolith growth and fish growth as fish age. The von Bertalanffy growth curve equation, $L_t = 138.9(1-e^{-0.25(t+0.79)})$, compared favorably with previous published values. Monthly changes in size and availability indicate a Gulf-wide migration of this moderately long-lived pelagic predator.

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The greater amberjack, *Seriola dumerili*, is a pelagic reef species ranging along the American coasts from Nova Scotia to Brazil and occurring throughout the Atlantic, Pacific, and Indian oceans, as well as the Mediterranean Sea (Mather, 1958; Burch, 1979; Shipp, 1988). It is the largest member of the family Carangidae (Hoese and Moore, 1977).

Commercial landings of amberjack (all species) have increased markedly over the past twenty years. Landings in the Gulf of Mexico peaked in 1988 reaching 2.7 million pounds, with a dockside value over 1.6 million dollars, but have since declined to less than one million pounds in 1995–96. Recreational catch statistics are incomplete but are suspected to have equalled or surpassed the commercial catch, raising concern over the status of the Atlantic stock in the late 1970s (Berry and Burch, 1979). Despite their popularity as a recreational and commercial quarry, little is known about the life histories of amberjacks (Shipp, 1988).

Of particular concern to stock-assessment scientists is the lack of age and growth estimates and population parameters for the amberjack family (Burch, 1979; Humphreys, 1986). Burch (1979), using scales, aged greater amberjack from the western Atlantic to 10 years for females and to eight years for males. Females were significantly longer than males beyond age four. Humphreys (1986) reported von Bertalanffy growth parameters for Hawaiian greater amberjack but did not elaborate on how the fish were aged or how many fish were contained in the data set.

The purpose of this study was to collect and describe greater amberjack otoliths, assess their utility in age estimation, and determine the size-at-age and growth rates of greater amberjack from the north-central Gulf of Mexico.

Materials and methods

Sampling

Greater amberjack (n=840) were collected off the Louisiana coast from April 1989 to June 1992. Sources of samples included a commercial processor plant (n=18), charterboats (n=352), saltwater fishing tournaments (n=215), spearfishing tournaments (n=159), recreational catches (n=48), and hook-

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and-line catches from an offshore gas production platform (n=48). In general sampling was not systematic; we examined all fish available.

Morphometric measurements and otoliths were collected. Fish were measured by using fork and total lengths (FL and TL) in mm and weighed by using total and gutted weights in g. Both sagittae were removed and stored in 95% ethanol for later examination. Lapilli, asterisci, and dorsal spines were removed from several fish to evaluate their usefulness for age estimation. Otoliths were cleaned of organic tissue by rinsing in a 50% hypochlorite solution (Clorox), air dried, weighed to the nearest 0.1 mg with a Sartorius model 1801 microbalance, and stored dry (Wilson et al.,1991).

Age estimates were made by using techniques similar to those of Wilson et al. (1991) for billfish. Whole otoliths were sputter coated with a mixture of gold and palladium and viewed with reflected light under a dissecting microscope for description of external morphology. These samples were also viewed with a Cambridge Stereoscan 150 scanning electron microscope (SEM) to obtain detailed photographs at magnifications ranging from 20 to 650×.

Sagittae were embedded in epoxy resin (Spurr, Embed 812, or Araldite GY 502) and sectioned with a Buehler Isomet low-speed saw to yield a thin (about 1-mm) transverse section containing the core (Beckman, 1989). Transverse sections were ground with various grades (300–2000 grit) of wet and dry sandpaper until the core was at the surface, then polished with 0.3 µm alumina polish. Thin sections were mounted on glass slides with a clear thermoplastic cement (Crystalbond 509) and viewed under transmitted light with an Olympus BH-2 compound microscope at 50–250× magnification. Age estimates from sectioned sagittae were made by combining counts of translucent and opaque zones and other growth features viewed under transmitted light and counts of associated ridges on the ventral and medioventral portions of the rostrum as determined in billfish species (Wilson and Dean, 1983; Prince et al., 1986; Wilson et al., 1991).

Validation and verification of our age estimation technique were attempted by using several techniques. Validation of annulus formation using marginal increment analysis proved futile owing to our inability to determine the condition of the otolith edge. Therefore we pursued additional techniques that would corroborate our age estimates. A mark-recapture study was carried out from a gas production platform (Mobil USA, West Cameron block 352) located in the Gulf of Mexico 50 miles south of Cameron, Louisiana. Greater amberjack (n=48) were captured by hook and line, measured as described above, tagged at the base of the dorsal fin with a Hallprint dart tag, injected with oxytetracycline hydrochloride (Agrimycin-100) at a rate of 20–40 mg/kg fish weight, and released. Tagged greater amberjack (6) were recaptured with hook and line or by spear fishermen at the release site and sampled as described above. Sectioned sagittae were viewed under ultraviolet light (405–435 nm wavelength) at 50–250× magnification for detection of the tetracycline mark. Attempts made to compare age estimates from sagittal otoliths with dorsal and anal spines and vertebrae were not successful. To determine reproducibility of age estimates, sagittae were aged independently by two readers. Reproducibility of age estimates was compared by using the coefficient of variation (CV) and index of precision (D) (Chang, 1982).

Tag-recapture data for the Gulf of Mexico and South Atlantic (n=711) were obtained from the Cooperative Gamefish Tagging Program (CGTP). Fish that had been at large for at least 365 days after tagging and that showed positive growth were used. Twenty-five specimens met these criteria. Following the method of Labelle et al. (1993), we used the von Bertalanffy growth curve parameters to predict changes in length from the tag recapture data to verify our age estimates. Like Labelle et al. (1993) we employed Fabens' (1965) length increment model to predict length at recapture:

$$lr_i = l_i + (L_\infty - l_i)(1 - e_i^{-k\Delta t}),$$

where l_i = length at release of individual i;
Δt_i = time of liberty of individual i;
lr_i = estimated length-at-recapture of individual i; and
L_∞ and k = von Bertalanffy parameters estimated from otolith ages.

Predicted recapture lengths were then compared with observed recapture lengths. As Labelle et al. (1993) pointed out, this procedure is not statistically rigorous but is useful for comparative purposes.

An analysis of variance (ANOVA) was used to test for sex-related differences in mean fork length, mean gutted weight, mean sagittal weight, and mean age among sources and within age class. Analysis of covariance (ANCOVA) was used to test for differences in the relations (fork length [L] versus total weight [Wt], fork length versus sagittal weight [SW], age versus sagittal weight) between sexes (Cerrato, 1990; Kimura, 1980). Statistical inferences were made with a significance level of α=0.05. The relationship between fork length and otolith weight was modeled with a negative exponential (von Bertalanffy) because it provided the best fit (highest r^2).

The von Bertalanffy model $L_t = L_\infty(1-e^{-k(t-t_0)})$ was also used to describe the relation between length and age. Relative ages were assigned to fish by using a birth date of 1 April based on trends in gonadosomatic indices and the regression of sagittal weight on month of capture for young-of-the-year fish.[1] Von Bertalanffy growth parameter estimates for males and females were compared by using a likelihood ratio test at $\alpha = 0.05$ (χ^2 statistic) (Cerrato, 1990; Kimura, 1980).

Results

Length and weight

Greater amberjack ranged from 167 to 1441 mm (FL); females ranged from 374 to 1441 mm ($\bar{x}$=879 mm), and males ranged from 387 to 1203 mm ($\bar{x}$=854 mm). Females represented 72% of the fish over 1 m in fork length. There was no significant difference in mean fork length between males and females. Females ranged from 0.82 to 42.5 kg ($\bar{x}$=11.33) and males ranged from 0.85 to 28.8 kg ($\bar{x}$=9.90). Mean gutted weight (GW) of females was significantly greater than that of males (ANOVA $P>F$= 0.03) and females represented 78% of the fish over 20 kg gutted weight. Regressions for TL versus FL and TW versus GW were

$$TL = 1.14\,FL + 13.05 \qquad (r^2=0.99)$$
$$TW = 1.09\,GW + 119.40. \qquad (r^2=0.99)$$

Monthly mean fork length and sex ratio from charterboat catches were compared because this was the only year-round source of greater amberjack (Table 1). Charterboats fishing Gulf of Mexico waters off the Louisiana coast caught larger greater amberjack during the summer months (from May to September) and smaller greater amberjack during winter months (from November to February). Sex ratios ranged from 0.4:1 to 4.5:1 ($\bar{x}$=2.49) (Table 1), and there was a relatively greater abundance of females each month except September.

The relation between fork length (cm) and gutted weight (kg) was best described by a power function. The slopes of the regression lines for males and females were significantly different. The equations explaining these relations were

All samples: $W = 4.2 \times 10^{-5} L^{2.83}$ (r^2=0.99, n=862)

[1] Thompson, B. A., C. A. Wilson, J. H. Render, M. Beasley, and C. Cauthron. 1992. Age, growth, and reproductive biology of greater amberjack and cobia from Louisiana waters. Final report to U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NMFS, St. Petersburg, FL, NA90AA-H-MF722, 77 p.

Table 1

Monthly mean fork length (mm) and sex ratio of charterboat-caught greater amberjack from the northern Gulf of Mexico ranked by decreasing mean fork length.

Month	Mean fork length (mm)	n	Sex ratio female:male
May	771.1	70	2.0
Jul	702.7	11	1.6
Jun	651.0	21	2.7
Sep	613.2	14	0.9
Mar	566.9	75	2.3
Apr	560.4	43	3.5
Nov	482.6	38	2.0
Oct	420.8	59	2.0
Feb	408.4	9	5.0
Dec	383.0	9	0.0
Jan	351.5	2	0.0

Females: $W = 3.25 \times 10^{-5} L^{2.87}$ (r^2=0.98, n=324)
Males: $W = 1.75 \times 10^{-5} L^{2.96}$ (r^2=0.98, n=184)
Sex unknown: $W = 7.62 \times 10^{-5} L^{2.87}$ (r^2=0.98, n=354)

Otolith structure

Greater amberjack sagittae are small, thin, fragile, and elongate in the anterior direction and bluntly crenelate at the posterior end. The medial surface is convex and has a deep, prominent sulcus. The anterior portion of the sagitta is curved laterally and the posterior end is relatively flat. The rostrum is longer than the antirostrum, but the difference increases with fish size. Prominent grooves and ridges are present on the lateral side of the sagittae and are nearly absent on the medial side (Fig. 1). The asteriscus and lapillus were much smaller and more fragile than the sagittae and have no annuluslike external or internal growth features. The small size and fragility of these smaller otoliths, as well as the time and care required to remove them, precluded additional sampling.

Greater amberjack sagittae weights ranged from 1.4 to 68.6 mg. The mean weight of male sagittae (23.2 mg) was not significantly different from that of females (25.0 mg). The relationship between FL and sagittal weight (SW) was best described with a negative exponential (following the von Bertalanffy equation). Because there was no difference in this relation between males and females ($P>\chi^2>0.05$) the data were combined to produce the equation (Fig. 2)

$$FL_{SW} = 151\,(1-e^{(-0.04(SW+1.6))}), \qquad (r^2=0.96)$$

Figure 1

Scanning electron micrograph of a sagitta (lateral view) (**A**), lapillus (**B**), and asteriscus (**C**) from a 42.7-cm greater amberjack from the north-central Gulf of Mexico.

where FL_{SW} = fork length (cm); and
SW = sagittal weight (mg).

Although internal annuluslike features were visible in whole otoliths, they were not sufficiently translucent to permit consistent enumeration. Readability was not improved by immersing sagittae in either glycerin or clove oil for up to one year. Surface grooves and ridges were prominent on the lateral side of sagittae from young fish but became compressed and indistinguishable in older specimens owing to an over-burden of calcium carbonate; a similar observation was reported for marlin (Wilson et al., 1991). External ridges were closely associated with internal microstructure that we interpreted as annuli. Although a first and second annulus was visible in whole sagittae, we concluded that annuli could not be enumerated from whole otoliths for most fish, particularly larger specimens.

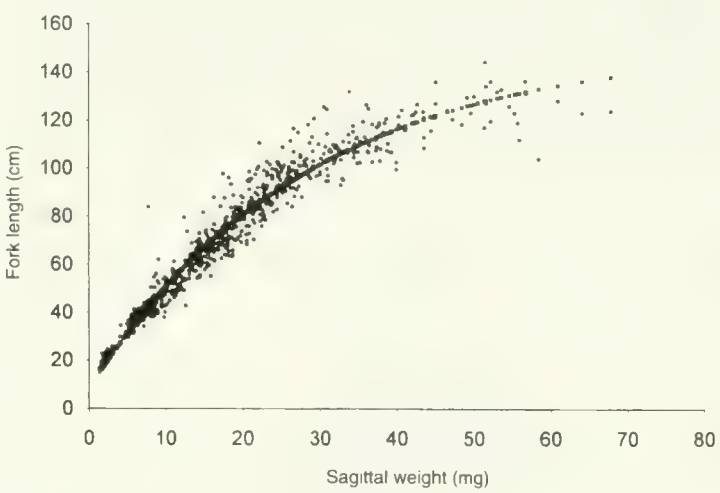

Figure 2

Sagittal weight (mg) versus fork length (cm) for north-central Gulf of Mexico greater amberjack. x represents predicted values from given equation.

Microstructural growth features were readily visible in most sectioned sagittae; however, the only consistent annuluslike features were regions where growth bands converged on the lateral side of the otolith section. These "convergence zones" were internal to the lateral surface of the antirostrum, where numerous growth features (increments) converged

on a common point (Fig. 3A); these features were usually associated with ridges on the lateral side of the sagitta or associated with alternating opaque and translucent zones, or with both ridges and zones (Fig. 3B). Similar structures were described and used to age istiophorids by Prince et al. (1986) and Wilson et al. (1991).

Six of 48 oxytetracycline-injected fish were recovered from the tag-recapture experiment. Oxytetracycline marks were observed in sectioned sagittae from all six fish (Fig. 4). The location of the oxytetracycline mark in relation to presumed annuli supported the use of the growth features described above. The specimen in Figure 4 was captured in September and recaptured in March and had an annulus consisting of a ridge and convergence zone between the tetracycline mark and the margin. The combined information obtained from six oxytetracycline-marked otoliths confirmed that one annulus is formed between November and March in the sagittae of two- and three-year-old greater amberjack.

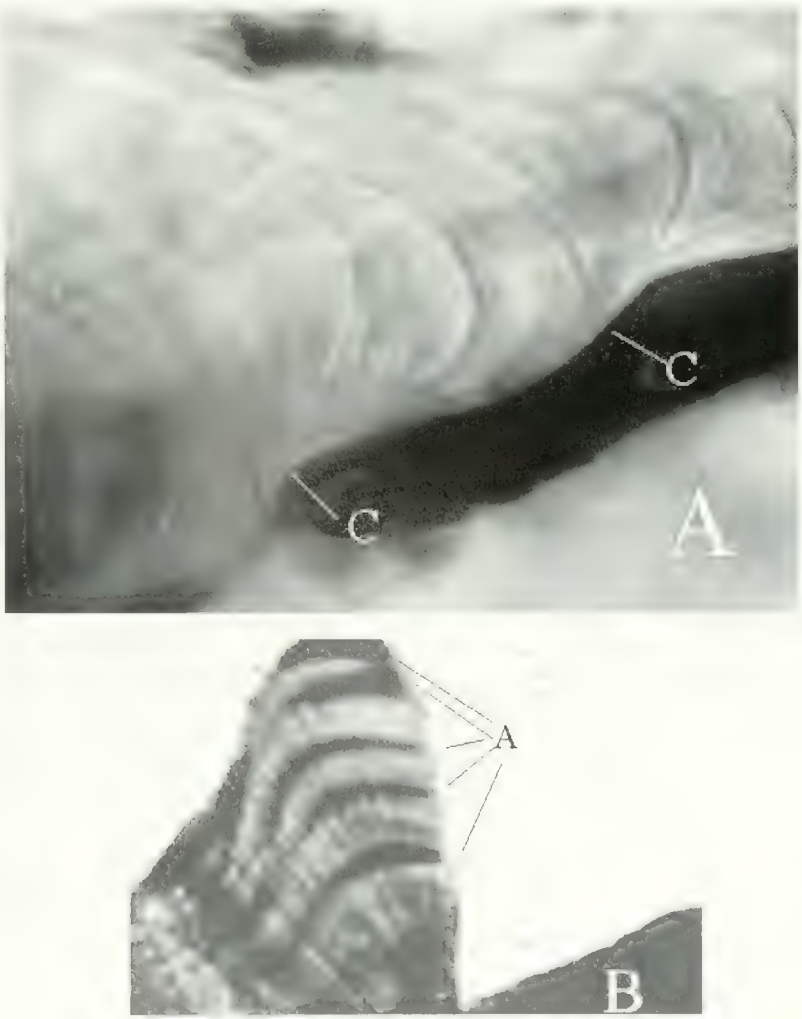

Figure 3

Photomicrographs of sectioned sagittae from a 72-cm-FL (**A**) and 42-cm-FL (**B**) north-central Gulf of Mexico greater amberjack. Photomicrograph A shows the convergence zones (C) along the dorsolateral edge of the rostrum. Photomicrograph B shows the opaque and translucent zones in the rostrum; opaque zones were interpreted as annuli (A).

Age structure

Five hundred and ninety seven greater amberjack sagittae were sectioned and aged by two readers. Forty-five specimens were considered unreadable owing to poor sample preparation. Pairwise comparisons between two readers indicated that 9.6% of the counts differed by 1 year, 1.6% differed by 2 years, and 0.4% differed by more than 2 years. Readers combined had a coefficient of variation (CV) of 0.15 and an index of precision (D) of 0.11.

Age estimates of greater amberjack ranged from young-of-the-year to 15 years. Mean age of males (2.9 yr) was not significantly different than that of females (3.2 yr) (ANOVA $P>F=0.064$); however, all fish over 9 years of age were female. Most of the greater amberjack sampled were from one to three years old (Fig. 5).

A linear function best described the relation between estimated age and sagittal weight. The regression parameters were not significantly different (ANCOVA) between males and females; therefore data were pooled and produced the relation

$$Age = 0.15(SW) - 0.44, \quad (r^2=0.75)$$

where SW = sagittal weight (mg); and
Age = amberjack age in years.

Growth was modeled by using the von Bertalanffy growth model (Fig. 6) to facilitate comparisons with other values reported in the literature. Our age data from

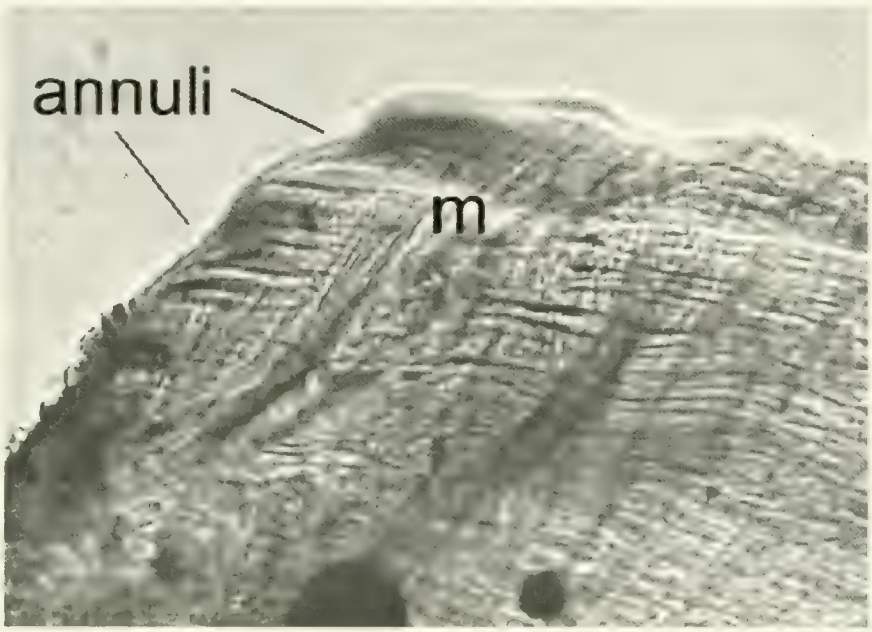

Figure 4

Photomicrograph of a sectioned sagitta from a 53-cm tagged and recaptured north-central Gulf of Mexico greater amberjack observed under ultraviolet light. The fish was at large for 160 days. Tetracycline mark = m; annuli are indicated by the arrows.

greater amberjack were fitted to the von Bertalanffy growth model (Fig. 7). Because there was no difference between male and female models ($P>\chi^2=0.496$), data were combined and resulted in

$$L_t = 138.9(1 - e^{-0.25(t + 0.79)}). \qquad (r^2=0.96,\ n = 552)$$

Tag-recapture data obtained from the CGTP yielded 25 data points useful for comparison of growth rates, and an additional six data points from our mark-recapture experiment. Predicted lengths fell along the trajectory of a line where predicted lengths equalled observed lengths (Fig. 7). The differences between observed and predicted values were both positive and negative. There was a tendency to under-predict fish size above 80 cm recapture length. The growth of tagged and recaptured fish provided additional support of our age estimation technique.

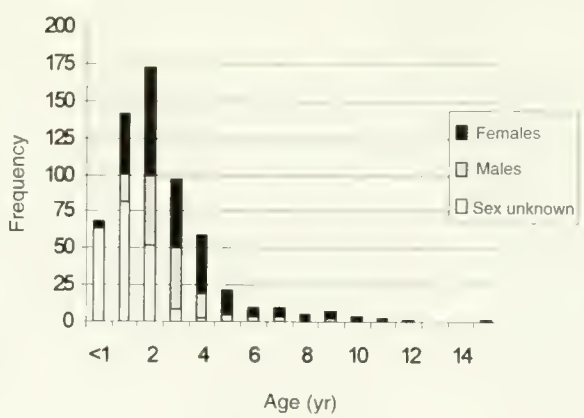

Figure 5

Estimated age-frequency histogram, identified by sex, of northern Gulf of Mexico greater amberjack collected from April 1989 to June 1992.

Discussion

Our observations of sex-related differences in maximum size of greater amberjack are consistent with the findings of previous investigators. Burch (1979) reported a maximum size of 145.0 cm for males and of 155.5 cm for females and noted that the mean fork length of females was greater than that of males of the same age. Humphreys (1986) reported a maximum size of 106.0 cm for males and of 149.4 cm for females. We found that the maximum size of males (132.7 cm) was less than that of females (144.1 cm) and that females represented 72% of the fish over

100 cm. Our data support the hypotheses that the maximum size in greater amberjack is sex related. Similar results were reported for other pelagic species (Atlantic and Pacific blue marlin, and swordfish) suggesting that females either grow faster, live longer, or both (Wilson, 1984; Wilson et al., 1991).

Charterboat-caught greater amberjack were collected year-round from the Louisiana coast, providing us with the opportunities to examine seasonal changes in the population. Size-frequency analysis of these data showed that fish were largest from May to September and smallest from November to February, suggesting a seasonal shift in the size frequency of individuals in the population off Louisiana. Although this seasonal size difference could be due to sampling bias, we believe that greater amberjack have an affinity for warmer waters and that the cooler waters associated with winter initiate an emigration from Louisiana waters. Burch (1979) reported greater amberjack migrating southward from December to May and northward from June to December in Florida. Baxter (1960) reported a northward migration of California yellowtail (as *Seriola dorsalis*) off California waters during early spring. The size at which greater amberjack begin to migrate is not known (Burch, 1979).

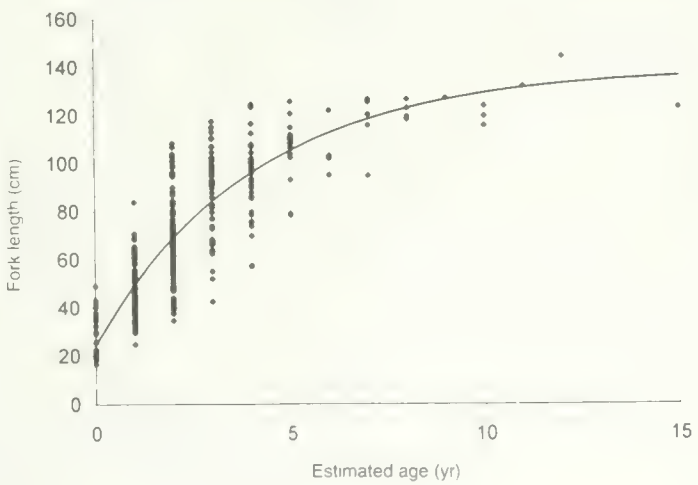

Figure 6

Plot of the estimated age and length of north-central Gulf of Mexico greater amberjack and the resultant von Bertalanffy relationship.

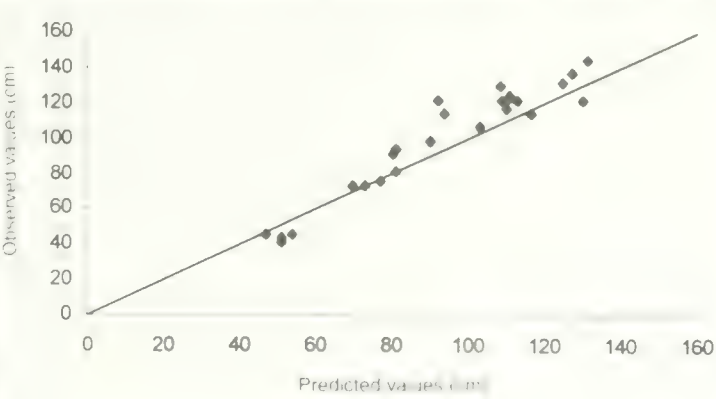

Figure 7

Predicted versus observed recapture lengths of tagged greater amberjack. Predicted values were calculated by using our von Bertalanffy growth parameters. The solid line covers points where the predicted and observed values are equal.

Females tended to be more abundant than males throughout our study, although the female-to-male ratio varied with time of year and source. This is contrary to Burch (1979) who reported female-to-male ratios from 0.6:1 to 2:1 with males more numerous in all months except July, August, and September. Humphreys (1986) reported a female-to-male ratio of 0.9:1. In our study, no trend in sex ratio was detected for charterboat-caught greater amberjack, and the overall ratio was 2.5:1. It is possible that males are more abundant off the west coast of Florida and females are more abundant off Louisiana. Thompson et al.[1] found that male cobia (*Rachycentron canadum*) dominated in the west-central Gulf of Mexico, whereas females dominated in the east-central Gulf of Mexico.

Otoliths

Greater amberjack otoliths are small, fragile, and complex in shape. In a comparison of external and internal features with those of other pelagic species, sagittae were found to be similar in shape to those of red steenbras (*Petrus rupestris*) (Smale and Punt, 1991), tunas (C.A. Wilson, unpubl. data), billfishes (Wilson et al., 1991), and several other carangids (*Alectis, Caranx, Chloroscommbrus, Elegatis*, and *Uraspis*, senior author, unpubl. data)

We tried several models (power function, logistic equation, Gompertz and Richards models) to describe the relationship between fish size (fork length) and otolith size (sagittal weight). A negative exponential in the form of the von Bertalanffy equation provided the best fit (r^2=0.96) and indicated that sagittal weight continues to

increase even after increases in fish length or weight slows or ceases (Pawson, 1990). This finding provides further evidence that otolith growth is more closely associated with time than with fish size as the fish becomes older. Secor and Dean (1989) suggested that otolith growth was a function of both somatic growth and time in young fish. We propose that as fish grow and approach an asymptotic size, otolith growth continues at a basal level and does not reach an asymptote. This is further evidence of the disassociation of otolith growth and fish growth in older fish. Continued sagittal growth throughout the life of the fish is the property that makes sagittae a useful ageing tool (Gamboa, 1991; Casselman, 1990).

Opaque zones (annuli) observed in transverse sections of greater amberjack sagittae were not as consistent as those reported in other species such as the sciaenids (Beckman, 1989; Casselman, 1990). Wilson et al. (1991) found that establishment of annual patterns in transverse sections of sagittae from pelagic fishes was best accomplished through interpretation of a combination of growth features on the surface of and in sectioned sagittae. Transverse sections of greater amberjack sagittae contained growth features described by Smale and Punt (1991) for red steenbras and by Wilson (1984) and Prince et al. (1986) for billfishes. We used similar criteria for discrimination of annual patterns in transverse sections of greater amberjack sagittae. Our criteria included external ridges on the lateral side of the sagittae, ridges within the sulcus acousticus, internal opaque and translucent zones, and the association of these features with a common area where many growth bands converged (Fig. 3A). All these growth features were coincident with annuli that were validated by using oxytetracycline-injected fish (Fig. 4). Smale and Punt (1991) found similar patterns in transverse sections of sagittae from red steenbras (*Petrus rupestris*). Although they reported fish as old as 25 years, transverse sections of sagittae from red steenbras looked similar to those of greater amberjack.

Disagreement over age estimates based on the above criteria was usually over an assignment of the first annulus. In some specimens a prominent opaque zone occurred adjacent to the core; we concluded it was laid down during the first winter and therefore did not consider it an annulus. Baxter (1960) reported that the first annulus was formed on the scales of yellowtail (as *Seriola dorsalis*) during their second winter, which was 18 months after hatching. We considered the first annulus in amberjack to be that which was laid down in the second year, when fish were actually 15 to 21 months old. When corrected for the discrepancy of the first annulus, the coefficient of variation and index of precision for the two readers were 0.15 and 0.11, indicating reasonable consistency in annulus interpretation. Similar values were reported by Wilson et al. (1991) for Atlantic blue marlin.

Apparently the sex-related size difference in amberjack is due to age-related differential mortality. Most of the greater amberjack collected were under 5 years old, although we found fish as old as 15 years. Males ranged from 1 to 9 and females ranged from 1 to 15 years. Females represented 76% of the samples above age 7. Burch (1979) found female greater amberjack to age 10 and males to age 8 for fish taken by southern Florida charterboat fishermen. The only other pelagic predator that demonstrates age-related sexual dimorphism, where females outlive males, is swordfish (Wilson and Dean, 1983). Greater amberjack also share a life history similar to both great barracuda and cobia in that they are all moderately long-lived pelagic reef species, and greater amberjack could be expected to exhibit similar patterns of longevity for males and females. However, deSylva (1963) found no age difference between sexes for great barracuda (*Sphyraena barracuda*). Richards (1967) reported no sex-related age differences for cobia (*Rachycentron canadum*) from mid-Atlantic waters, and Thompson et al.[1] reported similar findings for cobia from the Gulf of Mexico. We conclude that greater amberjack males die at a younger age than do females. More research is needed to determine whether these differences are real or are the result of sampling biases used in our study.

The relation between sagittal weight and age demonstrated that otolith weight can be used to estimate relative age. This finding is consistent with that for other pelagic species (Wilson, 1984; Wilson et al., 1991). Sagittal weight can provide a useful management tool because the random sampling and weighing of greater amberjack sagittae can be used to estimate age without the additional time and cost required for sectioning. We used a negative exponential to model the relationship between otolith size and fish size. The fit of this model indicates that otolith size continues to increase over time.

Growth

The von Bertalanffy growth parameter estimates obtained in our study were similar to both Burch's (1979) and Humphreys' (1986). Like Humphreys (1986), we did not find differences by sex. Burch (1979) reported L_∞ of 146.3 cm, 159.7 cm, and 164.3 cm for males, females, and sexes combined for charterboat- caught greater amberjack in Florida waters. Humphreys (1986) reported L_∞ of 149.3 for Hawaiian greater amberjack (sexes combined). We

obtained an L_∞ of 138.8 cm, slightly smaller than that obtained by other authors; differences may be due to duration of the growing season, because greater amberjack studied by other authors came from warmer climates where growth may have been more rapid. Our comparison of observed recapture lengths with predicted recapture lengths (Fig. 7) further verified our age-estimation technique. Of interest was our observation that this method tended to underestimate fish size at sizes larger than 80 cm. Because most of the tagged fish were collected off south Florida, it is possible that they grow slightly faster than those off Louisiana.

Conclusion

Our analysis provides evidence that greater amberjack from the north-central Gulf of Mexico are moderately long-lived, living up to 15 years. They demonstrate a sexual dimorphism, where females grow larger than males, but this appears to be age related because males die younger. Our use of sagittal annuli is validated for only two- and three-year-old fish and future studies will be needed to complete age validation.

Acknowledgments

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Mercury levels in four species of sharks from the Atlantic coast of Florida

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Florida's commercial and recreational shark landings represent a significant portion of the total U.S. Atlantic shark landings (NMFS, 1993). Shark landings have increased significantly during the past decade because human consumption of shark meat has become increasingly acceptable and because, in Asian markets, the demand for shark fins is very high—as are the prices paid for them (NMFS, 1993; Brown, in press). The east-central coast of Florida is an important area for commercial and recreational shark fishing, and a wide array of shark species, including those examined in this study, are landed in this region (Trent et al., 1997; FDEP[1]).

Mercury, a toxic metallic element, has been shown to bioaccumulate in fish tissue, and therefore, fish can represent a major dietary source of mercury to humans (Phillips and Buhler, 1978; Turner et al., 1980; Lyle, 1986). Methylmercury is the most toxic form of mercury for humans to consume (Meaburn, 1978; NMFS, 1993) and essentially all mercury found in fish muscle tissue (>95%) is in the monomethyl form (CH_3Hg)(Grieb et al., 1990; Bloom, 1992). Therefore, the measurement of total mercury provides an approximation of methylmercury and has been recommended as the standard for regulatory monitoring (Bloom, 1992). Elevated mercury concentrations in fish have been a growing concern among resource management agencies. Apex predators, particularly long-lived species such as billfishes (Förstner and Wittman, 1981; Barber and Whaling, 1983; Kai et al., 1987), tunas (Miller et al., 1972), mackerels (Meaburn, 1978), and sharks (Forrester et al., 1972; Walker, 1976; Lyle, 1986; Vas, 1991; Hueter et al., 1995, and others) have been reported to accumulate relatively high levels of mercury.

In May 1991, the Florida Department of Health and Rehabilitative Services (FHRS) released a health advisory urging limited consumption of all shark species from Florida waters.[2] Owing to mercury concentrations in excess of U.S. Food and Drug Administration and State of Florida standards, FHRS recommended "adults should eat shark no more than once a week; children and women of childbearing age should eat shark no more than once a month." State of Florida guidelines recommended that fish containing less than 0.5 ppm of total mercury should represent no dietary risk, fish containing 0.5 to 1.5 ppm of total mercury should be consumed in limited amounts, and fish containing greater than 1.5 ppm of total mercury should not be consumed. The 1991 health advisory regarding sharks in Florida waters was derived from a limited number of samples taken from retail sources and from studies that lacked important information regarding species, capture location, sex, and size of sharks examined. Increased landings of sharks in Florida for human consumption (Brown, in press; FDEP[1]) has prompted the need for more detailed information regarding mercury levels in Florida shark species.

Consequently, we report here analyses of total mercury levels in the muscle tissue of three carcharhinids (bull shark, *Carcharhinus leucas*; blacktip shark, *C. limbatus*; and Atlantic sharpnose shark, *Rhizoprionodon terraenovae*) and one sphyrnid (bonnethead shark, *Sphyrna tiburo*) from the east-central coast of Florida.

Materials and methods

Sample collection and mercury analysis

Sharks were collected during the Florida Department of Environmental Protection, Florida Marine Research Institute's Fisheries-Independent Monitoring Program in the Indian River Lagoon system and adjacent coastal waters or from commercial gillnet or longline fisheries operating in the nearshore

[1] FDEP (Florida Department of Environmental Protection) Marine Fisheries Information System, Fisheries Assessment Section, 100 Eighth Ave. SE, St. Petersburg, FL 33701.

[2] FHRS (Florida Department of Health and Rehabilitative Services). 1991. Health Advisory for Marine Fish. 1317 Winewood Blvd., Tallahassee, FL 32399, 3 p.

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Fish. Bull. 97:372–379 (1999).

and offshore waters of east-central Florida. All bull sharks were collected from estuarine nursery habitats within the Indian River Lagoon system from Oak Hill, Florida (approximately 28°52'N), south to the Ft. Pierce Inlet area (approximately 27°28'N). All blacktip, sharpnose, and bonnethead sharks were collected in nearshore and offshore waters from northern Cape Canaveral, Florida (approximately 28°55'N), south to the Sebastian Inlet/Wabasso, Florida, area (approximately 27°45'N). Samples were collected from 1992 to 1995.

Sharks were placed directly on ice and returned to the laboratory, where species, precaudal length (PCL), and sex were recorded. Stage of maturity was determined by examination of internal and external reproductive organs, as well as by comparison of shark size with estimates of size at birth or maturity from previous studies (Parsons, 1983, 1993; Branstetter and Stiles, 1987; Castro, 1996). Individuals were classified as neonates on the basis of unhealed or healing umbilical scars (Castro, 1993). To allow for comparisons with other studies, total length (TL), fork length (FL), and other morphometrics were also recorded according to Compagno (1984). With the exception of embryos, all sharks sampled were considered to be within the size range landed in Florida recreational or commercial fisheries. Axial muscle tissue samples were removed from the left dorsal area anterior to the origin of the first dorsal fin. White muscle tissue taken from this region is representative of the portion of shark used for human consumption. Tissue samples were immediately placed in sterile polypropylene vials, sealed, and frozen at –20°C until analyzed. Before analysis, tissue samples were digested by using standard procedures (EPA, 1991; Frick[3]) to convert all mercury in the sample to Hg^{+2}. The mercury in each digested sample was reduced to atomic mercury by reaction with excess stannous chloride. This atomic mercury was purged from solution in a gas-liquid separator and swept into an atomic absorption spectrometer for detection and quantification following standardized procedures (EPA, 1991; Booeshahgi et al.[4]) at the Florida Department of Environmental Protection's Division of Technical Services by using cold vapor atomic absorption spectrometry. Quality control measures included analysis of laboratory blanks, duplicate or triplicate tissue samples, and standard fish tissue reference material (DORM-1, obtained from the National Research Council of Canada) for each group of ten shark samples analyzed (EPA, 1991; Frick[3]; Booeshahgi et al.[4]). All mercury levels are reported as parts per million (ppm) wet weight.

[3] Frick, T. 1996. Digestion of fish tissue samples for total mercury analysis. Florida Department of Environmental Protection, Division of Technical Services, 2600 Blair Stone Road, Tallahassee, FL 32399. Report MT-015-1.

[4] Booeshahgi, F., M. Witt, and K. Cano. 1995. Analysis of total mercury in tissue by cold vapor atomic absorption. Florida Department of Environmental Protection, Division of Technical Services, 2600 Blair Stone Road, Tallahassee, FL 32399. Report MT-010-1.

Data analyses

Data regarding size and total mercury for each species were tested for normality by using the Kolmogorov-Smirnov test with Lilliefors' correction (Fox et al., 1994) and for homoscedasticity by using the F_{max}-test (Sokal and Rohlf, 1981) or by computing the Spearman rank correlation between the absolute values of the residuals and the observed value of the dependent variable (Fox et al., 1994). Linear regressions were used to describe relationships between shark size and total mercury concentration. Mercury data were log transformed to meet homoscedascity requirements. We used a *t*-test or Mann-Whitney rank sum test, as appropriate, to test for significant differences in total mercury levels and sizes between males and females for each species.

Results

Bull shark, *Carcharhinus leucas*

Eighty-three percent of 53 neonate and juvenile bull sharks (552–1075 mm PCL) tested from the Indian River Lagoon region had total mercury levels that were greater than or equal to the 0.5-ppm threshold level ($\bar{x}$=0.77 ppm; median=0.74 ppm; range 0.24–1.7 ppm) (Table 1). There was no significant difference between lengths of males ($\bar{x}$=735 mm PCL) and females ($\bar{x}$=754.6 mm PCL; *t*-test, $P>0.5$) nor was there a significant difference between mean total mercury levels between males and females ($\bar{x}$=0.76 ppm for both sexes; Mann-Whitney rank sum test, $P>0.05$). Ranges of total mercury for both sexes were also similar.

There was a significant positive correlation between total mercury level and bull shark length (both sexes combined) ($P<0.001$; Fig. 1). Total mercury levels in juvenile bull sharks increased as individuals grew larger, although some small sharks contained levels as high as those in larger sharks.

Blacktip shark, *Carcharhinus limbatus*

Total mercury levels for 21 juvenile and adult blacktip sharks examined ranged from 0.16 to 2.3 ppm

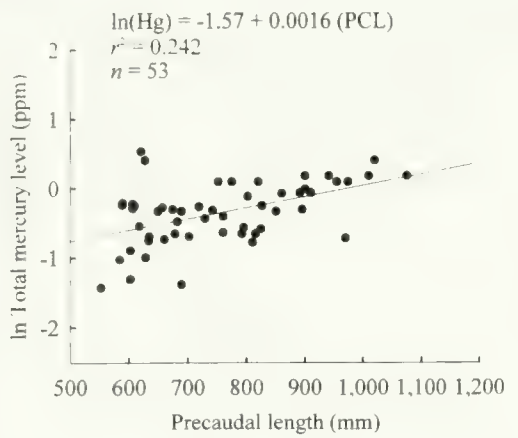

Figure 1

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile bull sharks, *Carcharhinus leucas*, from the Atlantic coast of Florida.

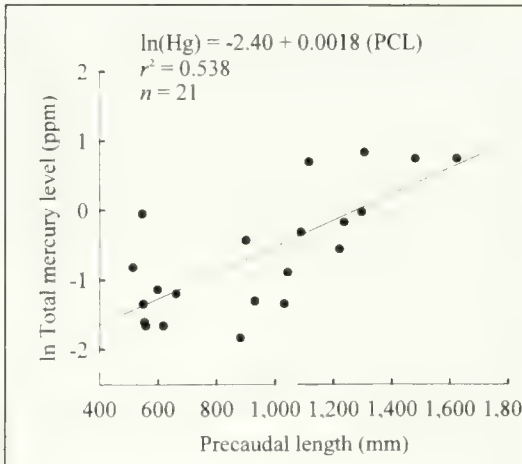

Figure 2

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult blacktip sharks, *Carcharhinus limbatus*, from the Atlantic coast of Florida.

Table 1

Total mercury levels in sharks from the Atlantic coast of Florida. *n* = number of sharks analyzed.

				Total mercury (ppm wet weight)			Precaudal length (mm)	
Species	Common name	*n*	Life history stage	Range	Mean	Standard deviation	Range	Mean
Carcharhinus leucas	bull shark	53	neonate/juvenile	0.24–1.7	0.77	0.32	552–1075	755.6
Carcharhinus limbatus	blacktip shark	21	juvenile/adult	0.16–2.3	0.77	0.71	513–1,623	939.6
		4	embryo	0.63–0.78	0.69	0.07	225–232	228.7
Rhizoprionodon terraenovae	Atlantic sharpnose shark	81	juvenile/adult	0.11–2.3	1.06	0.63	220–857	591.6
		6	embryo	0.17–0.29	0.22	0.02	74–85	80.3
Sphyrna tiburo	bonnethead shark	95	juvenile/adult	0.13–1.5	0.50	0.36	297–1081	590.3
		41	embryo	0.08–0.35	0.16	0.07	206–255	232.1

($\bar{x}$=0.77 ppm; median=0.44 ppm) (Table 1). Mean total mercury levels for females ($\bar{x}$=0.87 ppm) were higher than those for males ($\bar{x}$=0.58 ppm); however, these differences were not analyzed for statistical significance because sample sizes were small (n=14 females; n=7 males). The female blacktip sharks collected in this study were larger ($\bar{x}$=994.3 mm PCL) than the males ($\bar{x}$=830.1 mm PCL). Almost half (47.6%) of the blacktip sharks examined had mercury levels that were greater than or equal to the 0.5-ppm threshold level. The four blacktip shark embryos ($\bar{x}$=235 mm PCL), collected from a single 1050-mm-PCL female whose total mercury level was 2.3 ppm, had total mercury levels ranging from 0.63 to 0.78 ppm ($\bar{x}$=0.69 ppm; median=0.68 ppm) (Table 2). Mercury levels in these embryos equaled 27.4–33.9% of levels observed in their mother.

There was a significant positive correlation between total mercury level and blacktip shark length (both sexes combined)(P<0.0001; Fig. 2). Total mercury levels in blacktip sharks increased as individuals grew larger, although some small sharks contained levels as high as those in larger sharks.

Atlantic sharpnose shark, *Rhizoprionodon terraenovae*

Total mercury levels for 81 juvenile and adult Atlantic sharpnose sharks ranged from 0.11 to 2.3 ppm ($\bar{x}$=1.06 ppm; median=0.95 ppm) (Table 1). Although

Table 2

Total mercury levels of pregnant female sharks and associated embryos from the Atlantic coast of Florida.

	Pregnant female		Embryos		
Species	Precaudal length (mm)	Total mercury (ppm)	Precaudal length (mm)	Sex	Total mercury (ppm)
Carcharhinus limbatus	1050	2.3	230	M	0.78
			227	M	0.73
			235	M	0.63
			223	F	0.63
Rhizoprionodon terraenovae	766	1.9	84	F	0.29
			83	M	0.29
	782	1.6	76	M	0.17
			74	M	0.18
	784	2.3	85	F	0.19
			80	F	0.20
Sphyrna tiburo	990	1.1	229	M	0.12
			233	F	0.12
			236	F	0.14
	855	1	225	M	0.13
			237	F	0.19
			227	F	0.12
	1081	1.5	238	F	0.35
			230	M	0.14
Sphyrna tiburo	768	0.53	239	F	0.32
			229	F	0.30
			241	M	0.26
			224	F	0.28
			240	M	0.26
	877	1.1	238	F	0.11
			215	M	0.11
			228	M	0.13
			239	F	0.21
			230	M	0.10

females ($\bar{x}$=624 mm PCL) were significantly larger than males ($\bar{x}$=541.9 mm PCL) (*t*-test, $P<0.05$), total mercury levels of males ($\bar{x}$=0.92 ppm) and females ($\bar{x}$=1.15 ppm) were not significantly different (Mann-Whitney rank sum test, $P>0.1$). A total of 72.8% of all juvenile and adult Atlantic sharpnose sharks tested had mercury levels that were greater than or equal to the 0.5-ppm threshold level.

Total mercury levels for the six embryos (74–85 mm PCL) examined ranged from 0.17 to 0.29 ppm ($\bar{x}$=0.22 ppm; median=0.19 ppm). Mercury levels for embryos within each litter were very similar (Table 2) and equaled 8.3–15.3% of levels observed in their respective mothers. Overall mercury levels among litters were also similar (±0.02 SD). All confirmed pregnant females had levels greater than 1.0 ppm.

There was a significant positive correlation between total mercury level and Atlantic sharpnose shark length (both sexes combined)($P<0.0001$; Fig. 3). Total mercury level in this species increased as individuals grew larger. Total mercury levels for larger At-

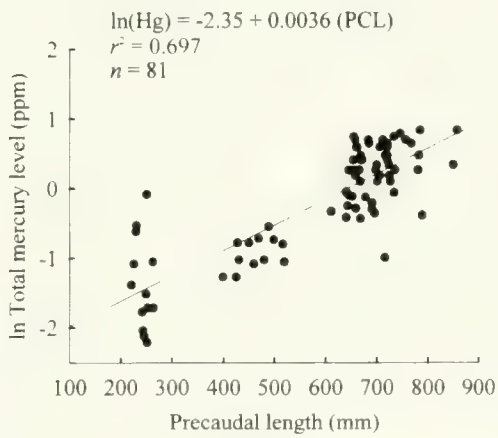

Figure 3

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, from the Atlantic coast of Florida.

lantic sharpnose sharks (>500 mm PCL) were always greater than 0.5 ppm.

Bonnethead shark, *Sphyrna tiburo*

Total mercury levels for the 95 juvenile and adult bonnethead sharks sampled (297–1081 mm PCL) ranged from 0.13 to 1.5 ppm ($\bar{x}$=0.50 ppm; median=0.29 ppm) (Table 1). Forty percent of all juveniles and adults tested had mercury levels that were greater than or equal to the 0.5-ppm threshold level. Mean lengths of males ($\bar{x}$=564.6 mm PCL) and females ($\bar{x}$=619 mm PCL) were not significantly different (Mann-Whitney rank sum test, P>0.1) and there were no significant differences in mercury levels between males ($\bar{x}$=0.49 ppm) and females ($\bar{x}$= 0.50 ppm) (Mann-Whitney rank sum test, P>0.5). There was a significant positive correlation between total mercury level and bonnethead shark length (both sexes combined) (P<0.0001; Fig. 4).

Total mercury levels for the 41 embryos examined (206–255 mm PCL) ranged from 0.08 to 0.35 ppm ($\bar{x}$=0.16 ppm; median=0.13 ppm). Mean length for male and female embryos were both 232-mm PCL. Total mercury levels of male ($\bar{x}$=0.15 ppm) and female ($\bar{x}$=0.18 ppm) embryos were similar (Table 2). Mercury levels for embryos within each litter were similar (± 0.03 SD)(Table 2), as were overall mercury levels among litters (mean mercury level/litter = 0.1–0.28 ppm). Total mercury levels in embryos of this species equaled 9.1–60.4% of levels observed in their respective mothers.

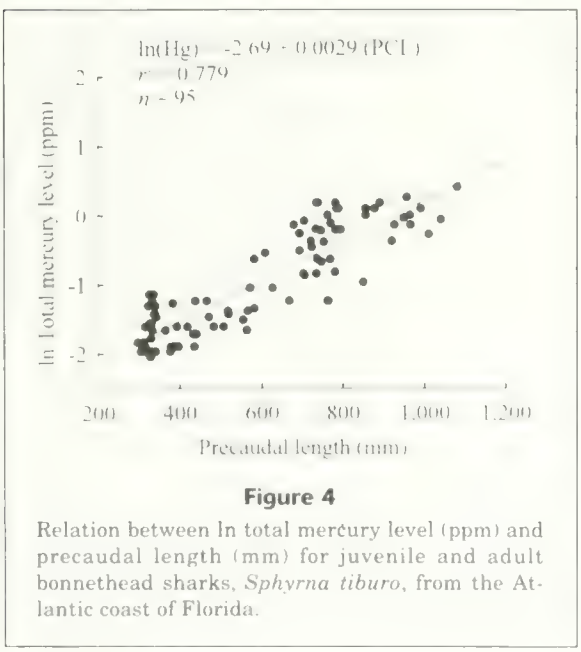

Figure 4

Relation between ln total mercury level (ppm) and precaudal length (mm) for juvenile and adult bonnethead sharks, *Sphyrna tiburo*, from the Atlantic coast of Florida.

Discussion

Results of this study indicated that most individuals in the four species of sharks tested had accumulated levels of total mercury that were as high as or higher than the regulatory threshold levels. Approximately 60% of the juvenile and adult sharks tested in this study had total mercury levels that were greater than or equal to the 0.5-ppm threshold level, and 12% had levels greater than 1.5 ppm. Information regarding mercury in sharks from other areas is limited; however, elevated levels of mercury in various shark species have been documented in several regions, including waters off Florida and the southeastern United States (Gardner et al., 1975; Hueter et al., 1995; FHRS[2]), Canada (Forrester et al., 1972), Great Britain (Vas, 1991), and Australia (Lyle, 1984, 1986). Although the life-history patterns of different shark species are diverse, most sharks grow slowly and have long lifespans. These general life-history characteristics, together with the high trophic status of many shark species, may contribute significantly to the accumulation of high concentrations of mercury (Lyle, 1984).

Mercury levels were directly related to shark size in all species tested. Length differences accounted for 78% of the total variation in mercury levels observed in bonnethead sharks, nearly 70% in Atlantic sharpnose sharks, and approximately 54% in blacktip sharks. The relation between mercury levels and length of juvenile bull sharks was less clear; length differences accounted for only 24% of the variation in mercury levels. The comparatively weak relation between mercury level and size in this species may stem from the fact that only neonates and small juveniles were sampled. Growth rates of bull sharks at the juvenile stage are thought to be quite variable (Dodrill, 1977; Thorson and Lacey, 1982; Branstetter and Stiles, 1987), which may explain some of the observed variability of mercury levels in juveniles of this species. For species we examined, the relations between total mercury and shark size demonstrated that larger, presumably older, individuals accumulated higher levels of mercury. The accumulation of mercury with increasing size and age is likely to be a result of the slow and inefficient elimination of mercury from fish tissue in relation to the rate of accumulation (Rodgers and Beamish, 1982; Bryan, 1984).

Because mercury levels increase as individuals grow larger, levels in juveniles can potentially be viewed as minima for the overall population. Although all bull sharks tested were either neonates or juveniles and the majority of blacktip sharks were juveniles or young adults, both species typically had

high mercury concentrations. High mean methylmercury levels (>1.0 ppm wet weight) were also detected in 29 larger size-class bull sharks (approx. 1300–2800 mm TL) and six blacktip sharks (> approx. 1500–1800 mm TL) collected off Florida (Hueter et al., 1995). Two of these bull sharks were collected off east-central Florida; however, specific size or sex data were not reported for these individuals. The observed relation of length to total mercury in juvenile bull sharks, together with results reported for larger size-class bull sharks and other closely related species (Lyle, 1984, 1986; Hueter et al., 1995), indicates that large adult bull sharks could contain excessive mercury levels. Blacktip sharks collected off northern Australia, which were of similar mean length and size range to those examined in our study, also had relatively high total mercury levels (Lyle, 1984, 1986). These data suggest that through bioaccumulation, larger, older adults of these common species potentially contain excessive mercury burdens. Total mercury levels for larger size-class Atlantic sharpnose sharks (>500 mm PCL) that we examined were consistently greater than 0.5 ppm. Muscle tissue from the related Australian sharpnose shark, *Rhizoprionodon taylori*, and the milk shark, *R. acutus*, tested from northern Australian waters (Lyle, 1986) contained mercury levels that were comparable to levels we detected in Atlantic sharpnose sharks. Milk sharks of comparable size examined by Lyle (1986) had total mercury concentrations (range=0.16–2.00 ppm wet weight; $\bar{x}$=1.01 ppm) that were very similar to those in Atlantic sharpnose sharks in the current study.

Bonnethead sharks had the lowest mean mercury content of the four species tested. The relatively low levels found in bonnethead sharks may be related to the comparatively fast growth rate and short life span of this species; however, diet is also an important factor. Bonnethead sharks off Cape Canaveral, Florida (senior author, unpubl. data), as well as off southwest Florida (Cortes et al., 1996), feed principally on crustaceans, whereas the other three species consume a larger proportion of fish (Compagno, 1984; Snelson et al., 1984; Castro, 1996; senior author, unpubl. data). Although available data are limited, crustaceans may contain mercury levels that are lower than those found in many fish species (Gardner et al., 1975; Stickney et al., 1975; Jop et al., 1997).

Mercury levels observed in embryos and neonates, as well as comparisons between pregnant females and associated embryos, indicated that transmission of mercury from maternal sources may be an important factor contributing to total mercury concentrations in shark muscle tissue. Total mercury levels in embryos of all species examined ranged from 8.3 to 60.4% of levels observed in their mothers, whose mercury levels were greater than the 0.5-ppm threshold (Table 2). Mercury levels of embryos within all litters were found to be similar. Mercury concentrations in embryos were variable among species. Atlantic sharpnose and bonnethead shark embryos all contained total mercury levels below the 0.5-ppm threshold; in contrast, all four embryos collected from a 1050-mm-PCL female blacktip shark had mercury levels greater than the threshold level. Variations in mercury concentrations found in embryos of different species could stem from differences in gestation periods or related physiological differences. Blacktip sharks have a two-year reproductive cycle with a 12-month gestation period (Castro, 1996), whereas Atlantic sharpnose sharks have a one-year reproductive cycle with a 10–11 month gestation period (Parsons, 1983). Bonnethead sharks have a gestation period of only 4–5 months (Parsons, 1993)—the shortest known gestation period of any placental viviparous shark species (Parsons[5]). This short gestation period, combined with other physiological factors and maternal diet may explain why bonnethead shark embryos contained the lowest mean mercury levels in this study. Walker (1976) suggested that transfer of mercury to developing ova and embryos may reduce mercury levels in mature females; however, little is currently known about maternal transmission of mercury in fishes. Mercury levels were relatively high in large females despite transfer of mercury to developing ova and embryos.

Results of this study indicate that the majority of sharks examined accumulated levels of total mercury that were greater than or equal to the threshold level of 0.5 ppm determined by the state of Florida. Mercury concentrations in adults and larger juveniles were typically elevated for all species; however, relatively high concentrations were also frequently observed in smaller juvenile bull and blacktip sharks. These data support the current health advisory in Florida urging limited consumption of sharks because of elevated mercury concentrations. Our data, in conjunction with the results of other studies conducted in the region (Gardner et al., 1975; Hueter et al., 1995; FHRS[2]), illustrate that mercury concentrations in several commonly landed shark species from the southeastern United States often exceed state and federal regulatory levels.

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A unique shell marker in juvenile, hatchery-reared individuals of the softshell clam, *Mya arenaria* L.

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The ability to identify individual bivalve mollusks in field populations is fundamental to understanding potential population regulatory mechanisms (such as the influence of population density, tidal height, and initial shell size on growth and survival rates, and fecundity schedules). Softshell clams, *Mya arenaria* L., have been commercially harvested from the soft-bottom intertidal zone in Maine since the mid-1800s and form the basis of an extensive fishery along its entire coast. Dramatic declines in landings during the past decade in Maine (Wallace, 1997), however, have resulted in attempts to use hatchery-reared juveniles to supplement wild stocks (Beal, 1994). In the past, distinguishing between cultured and wild bivalves in the field in order to follow their fate has been performed by using alizarin staining techniques (Newell and Hidu, 1982), by tagging individuals (Brousseau, 1979), or by applying colored marks (e.g. paint dots) to the valves (Peterson and Beal, 1989). Here, we describe a natural and unique shell marker for juvenile, hatchery-reared softshell clams that forms on the outer valves of individuals once they are placed in the field. The distinctive mark appearing on the surface of each valve obviates the need to apply physical tags to individuals and also eliminates the stress that small clams otherwise undergo when being tagged.

Methods

Clams were reared during the summer of 1983 at a 4-H clam hatchery in Jonesboro, Maine, and were held in running seawater in sediment-free trays at the Darling Marine Center, Walpole, Maine, until 25 May 1984. On that date, 5000 individuals (mean shell length [$\bar{x}_{SL}$ ±1 SD]=10.4 ±1.52 mm; range= from 6.7 to 14.6 mm; n=200) were transported back to the Jonesboro hatchery where the clams were divided into five groups of 100, 200, 300, and 400 individuals (i.e. a total of 20 groups). All but ten individuals from each group (20 groups× 10 individuals=200 clams) were marked with a single, group-specific, color-coded dot (Mark-Tex Corp. paint) on both valves near the umbo. The remaining 200 clams were painted with two dots to ensure individual recognition and measured (greatest shell length) to the nearest 0.1 mm by using vernier calipers. Marking was performed at this time because it was not known whether a distinctive mark would form naturally on the surface of each valve once clams began adding new shell in the field. Clams were maintained overnight without seawater at the University of Maine at Machias in a walk-in cooler (ca. 5°C).

On 25 May 1984, a matrix consisting of two rows of ten 0.25-m^2 plots was established near the midtide level of an intertidal flat (the Narrows) located along the western shore of the Chandler River (44°39'04"N; 67°33'10"W) near the town of Jonesboro, Maine. Sediments consisted of poorly sorted muds with a graphic mean ±1 SD of 3.6 ±0.34ϕ (n=2). The matrix was located approximately 55 m from the extreme high water mark and 35 m from the mean low water mark. Both rows were parallel to the shore and were spaced 1 m apart. Black rigid-mesh enclosures (DUPONT Vexar, 6.4 mm aperture), approximately 0.25 m^2 and 15-cm wide, were installed around each plot to restrict lateral movements of the small clams (Baptist, 1955). Because the enclosures had no mesh roofs, they allowed epibenthic and infaunal predators (*sensu* Commito and Ambrose, 1985) access to the clams (Peterson and Beal, 1989). The mesh of each enclosure wall was

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attached by staples to a 40 × 2.5 × 2.5 cm wooden stake at each corner. This square, fenced assembly was then pushed 8 to 10 cm into the sediments leaving a mesh wall projecting from 5 to 7 cm vertically.

Groups of clams were assigned randomly to the open enclosures on 26 May 1984. This completely random design resulted in five replicates of each of four evenly spaced planting densities ranging from 400 to 1600/m^2. The fate of the 200 clams marked with two dots is reported here (see Beal [1994] for results of increasing intraspecific density on the fate and growth of the remaining clams). To ensure that seagulls (*Larus* spp.) did not prey on the clams before they had the opportunity to burrow, one of us remained at the site until the tide had completely covered the clams and the enclosures. During this interval (ca. 2 hours) clams burrowed into the sediments approximately 20 minutes after planting. No clam was visible at the sediment surface at the time of tidal inundation.

Live and dead clams were recovered from each of the twenty open enclosures after 99 days (1 September 1984) by collecting the top 15 cm of sediment from each enclosure and sieving the sediment through a 0.5-mm mesh. For each live clam (marked with two dots or not), an obvious mark parallel to the entire shell circumference was visible on the shell at or near the size the animal was on 26 May 1984 (see "Results" section). This mark permitted us to estimate a shell growth index for every live clam:

$$\textit{Relative growth index} = [(\textit{final length} - \textit{initial length}) / \textit{initial length}] \times 100.$$

Index values greater than 100% indicate at least a doubling in growth.

Shells from this 1984 field experiment were not saved, but results from subsequent field trials in eastern Maine with hatchery-reared softshell clam juveniles (Beal, 1994) revealed that this shell mark remains visible for periods up to 1.5 years after planting. We used scanning electron microscopy (SEM) to describe the gross shell structure across the distinctive pre- and postplanting regions of the outer shell of juvenile, hatchery-reared clams. We used the valves of cultured clams (initial size similar to those reported above) that had been reared during 1989 at the Beals Island Regional Shellfish Hatchery (BIRSH), Beals, Maine, planted at the Narrows in May 1990 and recovered in October 1990. We also used SEM to examine the outer shell structure of wild juvenile clams (ca. 15 mm) taken from a nearby mudflat in Roque Bluffs, Maine, in September 1992.

Results

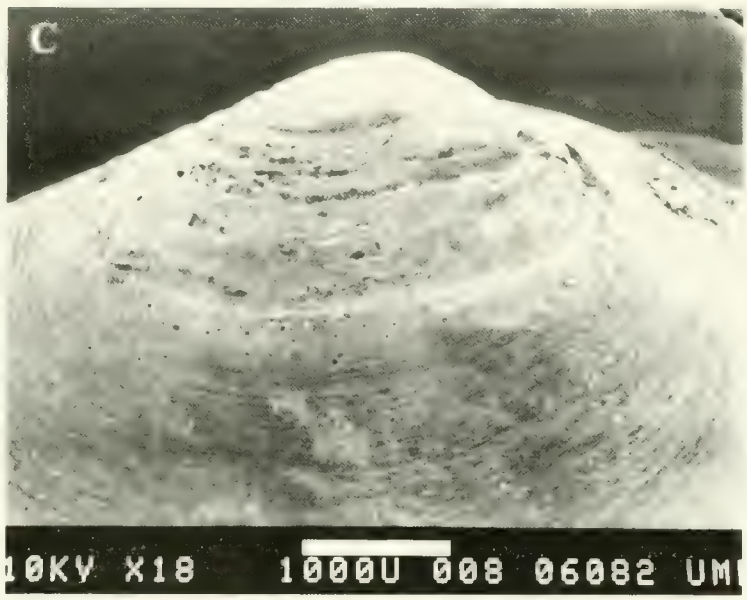
When viewed macroscopically, every live hatchery-reared clam taken on 1 September 1984 (regardless whether or not it had been marked with two dots) had a distinct line on its shell surface that appeared to correspond to its size at planting on 26 May 1984. Scanning electron microscopy (SEM) of the gross shell structure of wild juvenile clams (Fig. 1, A and B) revealed sharp ridges (=lines viewed macroscopically) approximately 15-microns apart punctuated by a relatively smooth region. In sharp contrast, the valves of cultured clams (Fig. 1, C and D) consistently revealed three distinct zones: an inner region from the umbo to a distinct area (line) of demarcation that was approximately 50-microns in width (Fig. 1D) and an outer zone from that line to the ventral margin. The inner zone was characterized by a pitted, amorphous surface with interrupted ridges, whereas the outer zone of the cultured clams (Fig. 1C) appeared similar to the entire surface of wild clams. Observations from experimental or stock enhancement outplantings of cultured clams from BIRSH in numerous coastal communities in Maine since 1987 indicate that the shell mark may be present for up to 1.5 years after planting (Beal, 1994).

To test whether the obvious line, or shell mark, could be used quantitatively to distinguish initial size at planting from subsequent shell growth, we examined closely the 57 surviving clams of the 200 that had been marked with two dots on 25 May 1984. We used calipers to estimate the initial size of the clam delimited by the obvious surficial shell mark (line). Next, we compared, for each clam, this estimate of initial (i.e. predicted) shell length with the one recorded on 25 May. If the hypothesis that the line is formed at or near the time of transplanting is correct, then the mean difference between actual (i.e. recorded) and estimated size should not be significantly different from zero. Results of a one-sample, two-tailed t-test demonstrated that the average difference was not significantly different from zero (–0.047 mm; t=–1.505; P=0.138; n=57). An alternative statistical approach is to plot the predicted initial shell length (y-axis) against the actual initial shell length (x-axis; Fig. 2) and to determine whether the straight line (y= –0.229 + 1.017x; r^2=0.97) is significantly different from the line $y = x$. The slope of the least squares equation for that line was not significantly different from unity (F=1.38; df=2, 55; P=0.26), and the intercept was not significantly different from zero (F=0.81; df=1, 55; P=0.37).

The mean relative growth index for the period 26 May to 1 September for the 57 marked survivors was 86.9 ± 2.26% SE (Fig. 3A). Mean final length of the same in-

Figure 1

Scanning electron microscopy (SEM) of the shell surface of a wild (**A** and **B**) and cultured (**C** and **D**) juvenile softshell clam, *Mya arenaria* (length ca. 15 mm). The wild clam was sampled from a mudflat in Roque Bluffs, Maine, in September 1992. The cultured clam was reared at the Beals Island Regional Shellfish Hatchery and planted in May 1990, in a mudflat at the mouth of the Chandler River, near the town of Jonesboro, Maine. Photo B, taken near the umbo region of the wild clam, shows uninterrupted concentric ridges and a lack of pits and amorphous grooves. Photo C is an example of "the hatchery mark." It is a continuous, ca. 50–micron groove that extends along the ventral slope (anterior to posterior) of both valves and appears at that point on the shell surface associated with the time the animal leaves the hatchery and is placed in the soft-bottom benthos. Photo D, was taken along the anterior–posterior groove that appears at the interface before the period when new shell is deposited once the individual is transplanted to the field. The white bar indicates a length of 1000 μ for A and C and 100 μ for B and D.



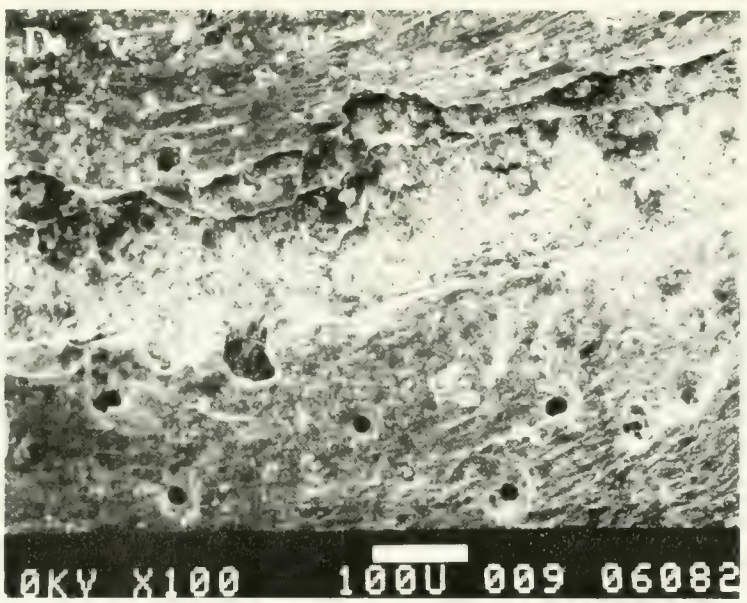


Figure 1 (continued)

dividuals was 19.6 ±0.24 mm SE (Fig. 3B), which equates to an average growth rate of 0.093 mm/day.

Discussion

Our data provide evidence of a distinctive mark or line being formed on the outer surface of the valves of juvenile hatchery-reared softshell clams. We have observed from other field tests and stock enhancement trials in Maine that the mark may be present for up to 1.5 years after planting, after which, the line disappears as the umbo region of the shell becomes increasingly worn, presumably on account of sediment abrasion from burrowing or seasonal repositioning (Zwarts and Wanink, 1989).

The formation of the line on the shell surface between the umbo and the ventral margin allows one to distinguish easily between wild and cultured juvenile clams and can be a valuable tool for resource

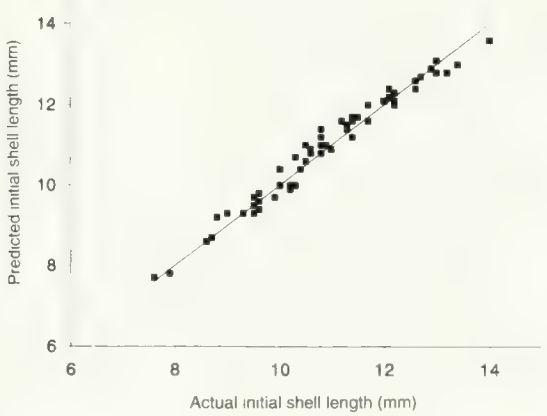


Figure 2

Predicted initial shell size versus actual initial shell size for the 57 hatchery-reared individuals of *Mya arenaria* marked with two dots that survived in open 0.25-m^2 field enclosures during the period from 26 May to 1 September 1984.

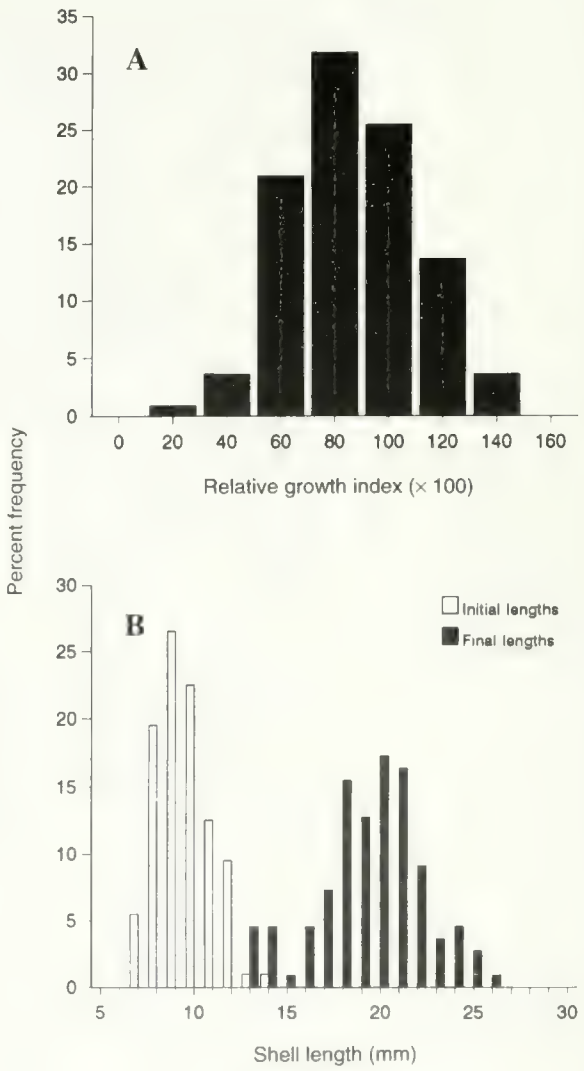


Figure 3

(**A**) Frequency distribution of relative growth rate index for the 57 hatchery-reared softshell clams marked with two dots (26 May to 1 September 1984). An index of 100% indicates a doubling of shell length. (**B**) Frequency distribution of initial (26 May 1984; n=200) and final shell lengths (1 September 1984; n=57) of hatchery-reared softshell clams.

managers wishing to assess the fate of hatchery seed for stock enhancement purposes (Beal, 1994). In addition, it obviates the need to mark (physically or chemically) individuals or a group. If initially unmarked, juvenile, hatchery-reared softshell clams are planted in the field and examined within an 18-month period, the distinctive shell mark allows one 1) to determine initial planting size of individual hatchery-reared clams (Fig. 2); 2) to determine relative or absolute growth rates (Fig. 3, A and B); and 3) to estimate the time (e.g. season) when death occurred for those individuals that suffered mortality after planting. Similar disturbance lines were observed on juvenile, hatchery-reared northern quahogs, *Mercenaria mercenaria* (L.), planted from the laboratory to various subtidal and intertidal sites in North Carolina (Beal, 1983).

The origin of the shell mark may be related to conditions within the hatchery environment. After the field experiment described above, cultured softshell clam juveniles from BIRSH were planted in intertidal flats along the coast of Maine (1987–94) during the months of April through October for both manipulative tests and community-based stock enhancement efforts (Beal, 1994). In addition, cultured clam stock produced in a commercial shellfish hatchery (Mook Sea Farm, Inc., Walpole, Maine) were used in stock enhancement programs in Gloucester and Ipswich, Massachusetts (Whitten[1]). Regardless of hatchery origin, the same line appeared on the shells of all survivors planted in the soft-bottom intertidal zone at all locations, as well as on shells of those that grew before dying.

The mark has been observed in clams planted at shell sizes as small as 3 mm and as large as 25 mm (Beal, 1994). In addition, this mark appears regardless whether clams are transplanted to the field directly from the hatchery or are overwintered in submerged, floating cages (*sensu* Beal et al., 1995) before transplanting to the field.

[1] Whitten, J. 1996. Merrimak Valley Planning Commission, Haverhill, MA. Personal commun.

Although not specifically tested, at least two competing hypotheses may explain the mechanism that creates this shell marker. The first hypothesis is disturbance, for clams in the hatchery are grown in sediment-free trays with fine-mesh screening (150–1500 μ), handled (sieved) weekly, fed tropical species of microalgae such as *Isochrysis galbana* (Tahitian variety), and are grown at temperatures between 20 and 25°C—well above those normally experienced in the wild in eastern Maine. Once they have left the hatchery environment, clams are planted on flats and immediately burrow into sediments where 1) hatchery-produced disturbance ends, 2) the clams begin feeding on natural phytoplankton assemblages, and 3) they experience seawater temperatures that typically do not exceed 17°C. The new shell that grows is always distinctly whiter than the older shell. This difference in coloration may indicate a release from competition for calcium or aragonite which may be limited under hatchery conditions (Barber[2]). The second hypothesis is bacterial damage that may also relate to conditions in the hatchery where elevated levels of marine bacteria such as *Vibrio* spp. frequently occur. Qualitative tests for the presence of *Vibrio* spp. (using Difco TCBS agar [Elston et al., 1981]) at BIRSH are made regularly and show a general presence of these bacteria in the seawater within tanks holding juvenile clams, in the cultured algae, and on the valves of juvenile clams. These gram-negative, oxidase-positive, fermentive rods have been observed similarly in commercial bivalve hatcheries in the coastal northeastern United States (Elston, 1984) where they have been described as coating the shell surface of cultured juvenile northern quahogs, oysters, *Crassostrea virginica* (Gmelin), *Ostrea edulis* L., and bay scallops, *Argopecten irradians* (Lamarck). Bacteria in the family Vibrionaceae can erode and perforate areas on the surface of bivalve shells through the production of a variety of acidic metabolites that are inimical to normal deposition of calcium carbonate (Elston et al., 1982). The SEM photograph of the valve of the hatchery-reared softshell clam (Fig. 1, C and D) clearly shows pitting and amorphous grooves that may indicate a bacterial origin.

During the past decade, clam landings in eastern Maine have declined by nearly 75% (Wallace, 1997). Communities that manage their clam stocks in this and other regions along the coast are beginning to use cultured softshell clams to enhance clam production. Testing the biological and economic efficacy of hatch-and-release programs is critical for the development of sensible management programs. Results presented here demonstrate the ease of distinguishing cultured from wild *Mya* and will allow scientists as well as clam harvesters a rapid assessment of field planting programs.

[2] Barber, B. 1994. University of Maine, Orono, ME. Personal commun.

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Occurrence of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, in the northeastern Gulf of Mexico

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The sandbar shark, *Carcharhinus plumbeus*, is a large, coastal species of the western north Atlantic occurring from Cape Cod, Massachusetts, to Brazil, including the Gulf of Mexico and Caribbean (Bigelow and Schroeder, 1948; Springer, 1960). Sandbar sharks are targeted by commercial fisheries and account for up to 60% of the large coastal shark landings in U.S. southern waters (NMFS, 1993). Adults are highly migratory and mostly congregate offshore. Neonate and juvenile sandbar sharks, on the other hand, are commonly found in coastal nursery areas where they feed (Medved et al., 1985) and avoid predation (Springer, 1967; Branstetter, 1990) during summer months.

The presence of neonate and juvenile sandbar sharks has been well documented in coastal areas of the eastern United States. Springer (1960) reported juvenile sandbar sharks from Cape Cod, Massachusetts, to Cape Canaveral, Florida. Juvenile sandbar sharks are abundant in Chesapeake Bay and eastern shore of Virginia in less than 10 m (Medved and Marshall, 1981; Musick et al., 1993). Castro (1993) found neonate and juvenile sharks in Bulls Bay, South Carolina. Pratt and Merson[1] determined Delaware Bay, New Jersey, as a major nursery area for neonate and juvenile sharks. Further attempts to delineate the extent of nursery areas for sandbar sharks along the U.S. east coast continue (Damon, 1997; Pratt and Merson[1]).

Juveniles are not known to occur in coastal areas of the eastern Gulf of Mexico. The direct correlation of juvenile sandbar shark survivorship and future stock size (Cortés, in press) requires delineation of sandbar shark nursery areas. Thus, if recruitment to the stock is assumed to be entirely from sharks from the U.S. east coast, then underestimates of total population size could occur and affect overall stock assessments. This paper reports on the occurrence of neonate and juvenile sandbar sharks and the potential nursery area of these sharks in coastal waters of the northeastern Gulf of Mexico.

Materials and methods

Sandbar sharks were captured from October 1992 to October 1997 as part of studies on the distribution and abundance of sharks in the eastern Gulf of Mexico. Because sampling had various objectives, the variability in sampling design and methods precluded quantification of a valid time series of abundance (e.g. CPUE) from 1992 to 1997. In general, gill nets varied in height from 1.52 to 3.04 m and ranged in length from 30.4 to 273.6 m, and mesh sizes from 6.9 to 20.3 cm stretched mesh. Each net, regardless of size, was anchored at both ends and fished on the bottom. Longlines, which ranged in length from 76 to 335 m and consisted of 10–60 hooks, were anchored at both ends and fished so that one half fished the "midwater" and the other the "bottom." Gangions were 0.9–1.8 m long and hooks were size 3/0 and 12/0 (Mustad). Usually menhaden (*Brevoortia* spp.) was the bait of choice.

The nets or longlines, or both, were set over a 24-h period at various times. Gill nets and longlines were checked, or checked and pulled, and sharks were removed throughout each sampling period. Surface water temperature (°C), salinity (ppt), and light transmission (cm) were measured daily at each station.

After they were caught, sharks were sexed and measured (total length, TL) to the nearest mm. Sharks that were in poor condition were euthanized for life history information; those in good condition were tagged with a multirecapture, nylon-head, dart tag (Hueter and Manire[2]) and released. Sampling took place April to October of each year, occasionally from November to March.

Study area

Sampling sites were located in four major areas along the northeastern portion of the Gulf, Apalachee Bay to St. Andrews Bay, Florida (Fig. 1).

[1] Pratt, H. L., and R. R. Merson. 1996. Delaware Bay sandbar shark nursery pilot study. Narragansett Laboratory, National Marine Fisheries Service, NOAA. Progress report, 23 p.

[2] Hueter, R. E., and C. A. Manire. 1994. By-catch and catch-release mortality of small sharks and associated fishes in the estuarine nursery grounds of Tampa Bay and Charlotte Harbor. NOAA NMFS/MARFIN Program. Project Rep. NA17FF-0378-01, 183 p.

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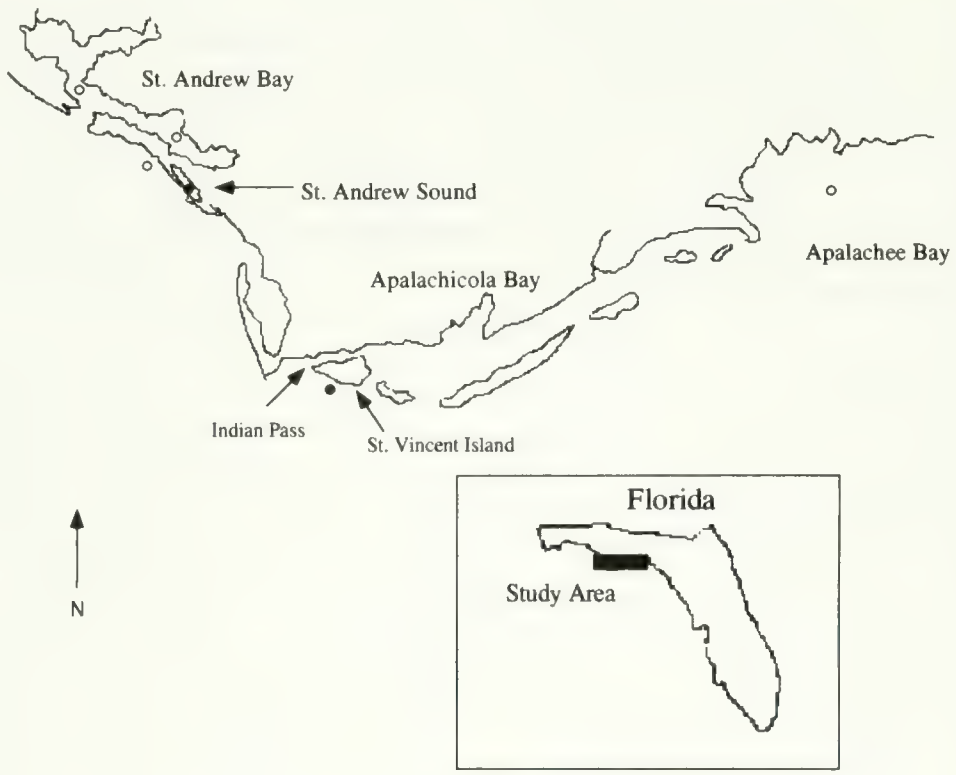

Figure 1

Map of the study area in northwest Florida near latitude 30°00'N and longitude 85°35'W illustrating the major sampling areas (o) and the two areas (•) in which sandbar sharks were captured from October 1992 to October 1997.

The eastern part of this area has an irregular coastline, few beaches and enclosed bay systems, and has large amounts of submergent (*Thalassia* spp. and *Halodule* spp.) and emergent vegetation (*Spartina* spp. and *Juncus* spp). The western part has numerous barrier islands and sand beaches and is composed of semi-enclosed bays. Tidal amplitude in the bays is highest in Apalachee Bay and generally decreases toward the west.

St. Andrew Bay consists of several embayments (average range 1.9–5.7 m deep) and has low freshwater inflow, low turbidities, and high percentages of sand in the substrate. Salinity ranges from 13 to 32 ppt and tidal amplitude averages 0.48 m. The system exchanges water with the Gulf of Mexico through two passes, a natural pass at the east end and a man-made pass at the west end.

St. Andrew Sound is a small semi-enclosed marine lagoon with expanses of submergent vegetation. It is about 14.5 km long and 0.2–2.0 km wide and has water depths from 3.5 to 4.5 m deep (mean high tide). Salinity ranges from 25 to 36 ppt and tidal amplitude averages 0.42 m. The sound exchanges water with the Gulf of Mexico through a pass (≈0.5–2.0 km wide) that was created near the center of Crooked Island by Hurricane Eloise in 1975.

Indian Pass is located at the western end of the Apalachicola Bay system. This area is about 2–3 km south of St. Vincent Island in the Gulf of Mexico where the average range of water depth is 5–10 m. The bay system surrounding this area is largely a line of barrier islands fronting the intersection of the Apalachicola delta and is the only bay system in Florida in which a large river system drains. As a result of river discharge, there is little submergent vegetation due to high turbidity. Salinity fluctuates from 15 to 35 ppt and tidal range is 0.66 m.

Apalachee Bay is an open ocean bay without barrier islands separating the area from the open Gulf of Mexico. The bay is broad, shallow (average 3 m), and extends about 15 km offshore. Salinity ranges from 22 to 36 ppt and tidal amplitude averages 1.0 m. Wave energy is low and the area has large expanses of submerged vegetation.

Results

Neonate and juvenile sandbar sharks (n=105) were captured in two areas of the northeastern Gulf of Mexico, Indian Pass, and St. Andrew Sound. Captured sandbar sharks were 572–1640 mm TL (Fig. 2). Seventeen were determined to be neonates and young-of-the-year (mean size=643 ±44.5 mm TL), as indicated by the presence of an open or partially healed umbilical scar. The largest sandbar shark with a partially healed umbilical scar was 720 mm TL. Following the age-length relationship provided in Sminkey and Musick (1995) and the life history stage classification in Cortés (in press) we estimated that 52 sharks were small juveniles (about 1–3 yr old), 34 were large juveniles (about 4–9 yr old), and 2 were subadults (about 10–12 yr old). Mature adults were not caught.

Sandbar sharks were captured in all years except 1995 (Fig. 3). The number of individuals collected was highest in 1993. Small juveniles were the dominant life stage captured in 1993 and 1997 and larger juveniles in 1994. Young-of-the-year, including neonates, were caught in all years sandbar sharks were captured.

The abundance and size of sharks varied with season (Fig. 4). Sandbar sharks were not captured until April when the water temperature approached 22°C. These were mostly small juveniles ranging in size from 800 to 1200 mm TL. Neonates were first captured in June when temperatures reached 25°C and young-of-the-year continued to be caught through October.

There was a significant relationship between abundance and water temperature (r^2=0.25, P=0.008), but not with salinity or turbidity (P≥0.05). Sandbar sharks were most abundant during summer months when all size classes were caught. Few larger juveniles were caught in fall.

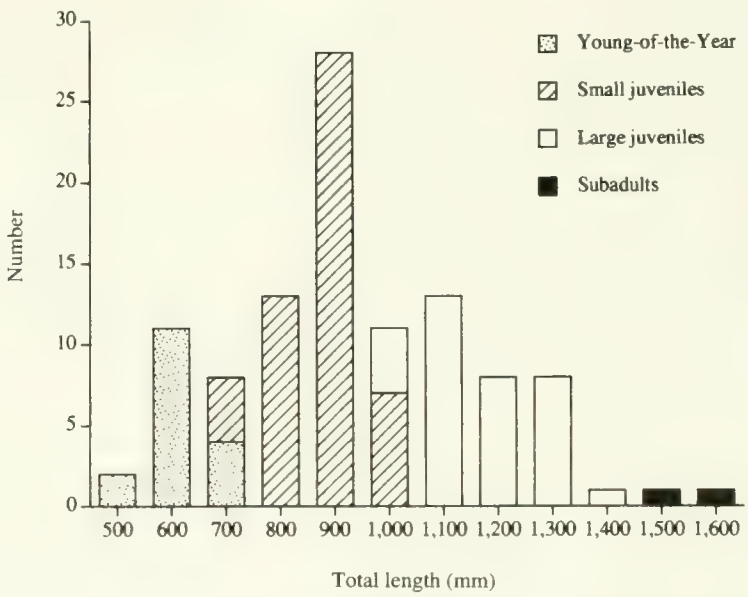

Figure 2

Length-frequency distribution of all sandbar sharks (n=105) by life history stage caught in gill nets and longlines from October 1992 to October 1997. Young-of-the-year includes neonates.

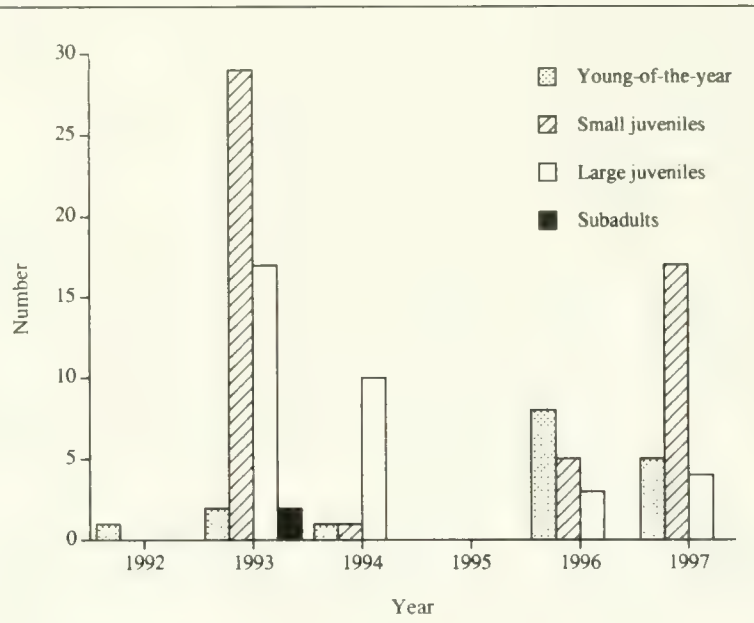

Figure 3

Overall abundance of sandbar sharks captured by year and life history stage from October 1992 to October 1997. Young-of-the-year includes neonates.

Discussion

Presence of neonate and juvenile sandbar sharks in the northeastern Gulf of Mexico suggests that sandbar sharks pup in the eastern Gulf of Mexico. Springer (1960) proposed the existence of two breeding populations of sandbar sharks, one off the mid-Atlantic coast

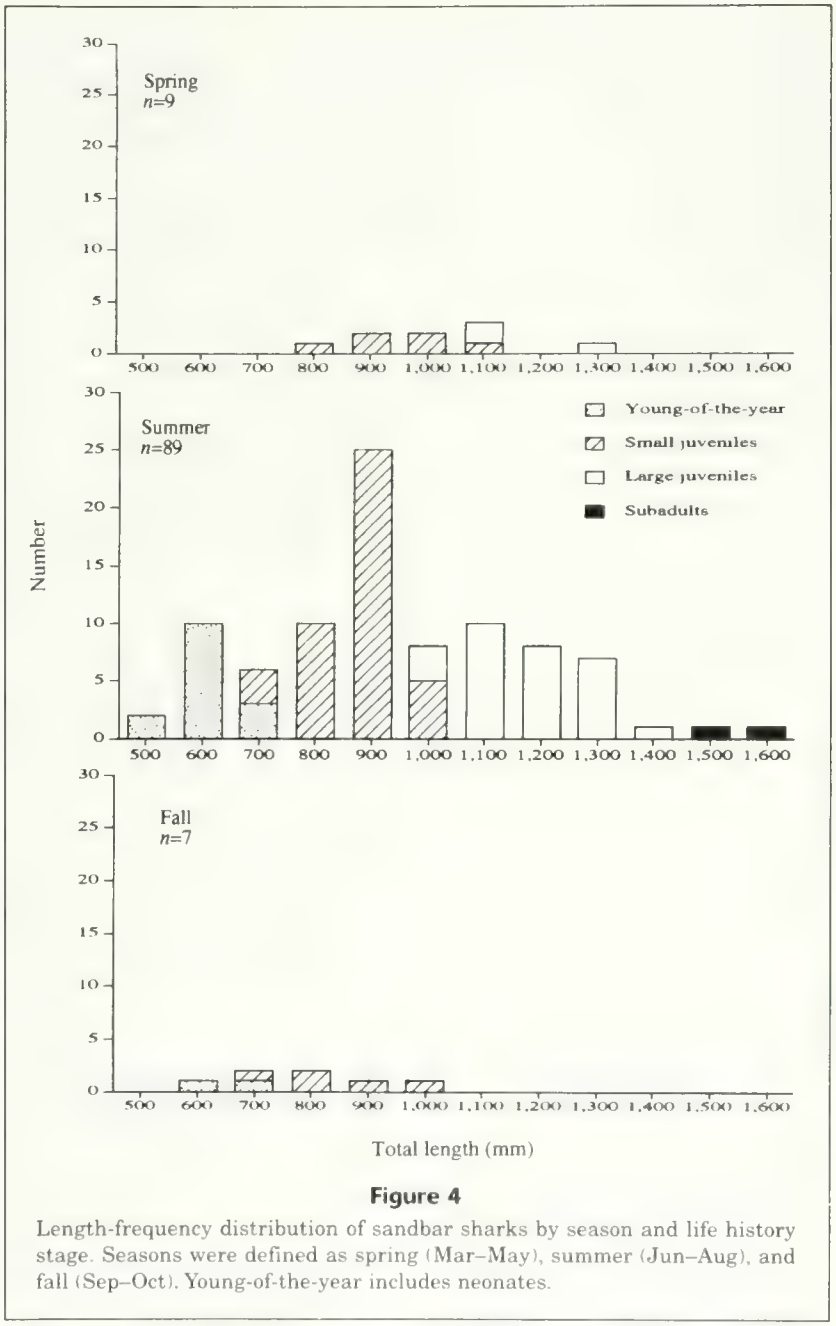

Figure 4

Length-frequency distribution of sandbar sharks by season and life history stage. Seasons were defined as spring (Mar–May), summer (Jun–Aug), and fall (Sep–Oct). Young-of-the-year includes neonates.

of the United States, one in the western Gulf of Mexico. Bigelow and Schroeder (1948) captured one sandbar shark that was 747 mm TL off the Texas coast, and Springer (1960) took a few females with full-term pups near the mouth of the Mississippi River. Branstetter (1987) captured two neonates (67 and 69 cm TL) from Galveston Bay, Texas. Some evidence of possible pupping areas in the eastern Gulf of Mexico was presented by Clark and von Schmidt (1965), who captured gravid females off Sarasota, Florida, and Branstetter (1981), who reported on six gravid females from a Shark Rodeo off Pensacola, Florida. However, no neonate or juvenile sharks have been previously reported from the eastern Gulf of Mexico.

Sandbar shark distribution in the northeastern Gulf of Mexico was limited to the mouth of the Apalachicola River, near St. Vincent Island; none were caught in three additional areas sampled and only two were captured in St. Andrew Sound. Although all areas sampled vary in environmental parameters, none of the environmental conditions measured appeared to be associated with the distribution of juvenile sandbar sharks. It is possible that sandbar sharks are attracted by the abundance of

prey and bycatch from intense commercial shrimping operations that occur in the area surveyed at the mouth of the Apalachicola River.

The absence of gravid females in the survey does not preclude the presence of a pupping and nursery area. Females may be pupping farther inshore or offshore from the sampling area, at times when sampling did not occur or sampling gear may have had reduced efficiency at capturing larger sharks. Female sharks are reported to move into Chesapeake Bay to pup when water temperatures reach 18–20°C (Grubbs, 1996), and most sampling in this study began in April when water temperatures were usually above 20°C. In addition, mature female sandbar sharks are large (>1800 mm TL; Sminkey and Musick, 1995) and it is likely that they were able to avoid the sampling gear.

Neonate sandbar sharks (<age 1) usually reside in primary nursery areas where they were born through the first summer (Pratt and Merson[1]); thus it is unlikely that individuals captured in this area underwent significant migrations from another area. The paucity of tag and recapture information in the Gulf of Mexico also complicates understanding of the geographical and seasonal distribution of neonate and juvenile sandbar sharks. Future research should be focused on further delineation and annual monitoring of hypothesized nursery areas for sandbar sharks and on increasing ongoing tagging efforts.

Acknowledgments

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Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount

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Aggregations of tuna can be found in association with seamounts throughout all the tropical oceans and these aggregations are often exploited by tuna fishing fleets (Fonteneau, 1991). In Hawaii, a fishery has developed over the last decade that targets the mixed species aggregations of predominantly subadult tuna found in association with the Cross Seamount located approximately 160 nmi south of Honolulu and Oahu and 150 miles east of South Point on the island of Hawaii (Fig. 1). Its shallowest depth is about 330 meters.

The Cross Seamount fishery is a hybrid troll, jig, and handline fishery that augments slow trolling methods by using frozen, cut and whole bait to induce feeding behavior around the fishing boat. Initially described as a yellowfin tuna (*Thunnus albacares*) fishery, closer scrutiny has revealed that the catch is dominated by juvenile bigeye tuna (*T. obesus*). Schools of skipjack tuna (*Katsuwonus pelamis*) are also found over the seamount but these are avoided by fishermen and, when skipjack tuna occur in mixed schools with the other species, the quite large size of the baits deters the capture of skipjack tuna. The fishery occurs year-round but fishing effort tends to subside periodically when larger tuna become available closer to shore—primarily during summer months.

Two concerns have arisen within the fishing community. First, fishermen exploiting the Cross Seamount resource were concerned that increasing fishing effort at the seamount by additional vessels entering the fishery would overexploit the schools of tuna associated with the seamount. Second, there was concern among the broader community that heavy fishing effort at the seamount might reduce the number of fish that were available to other gear types operating closer to shore. That is, the seamount might be a major "staging point" for fish that subsequently move into the coastal handline and troll fisheries. In response to these concerns, a tag-and-recapture program was conducted to elucidate the dynamics of the tuna populations associated with the seamount and to document the movements of individual fish forming those aggregations.

Materials and methods

Tag-and-release operations were conducted by trained tagging technicians placed onboard collaborating commercial vessels. Tuna were caught by crew members using handlines and pole-and-line methods, and the fish were then passed to the tagging technician for evaluation, identification, measurement, and tagging. Standard, serially numbered 11-cm nylon-tipped dart tags (Hallprint Pty, Australia) carried a message (stating a reward) and a toll-free phone number for reporting recaptured fish. Also, because the commercial fishing fleet in the seamount fishery consists of fewer than ten boats, close liaison was established with these boats to ensure maximum reporting of fish recaptured at the release site.

Residence times for tuna at the seamount were calculated by constructing tag-recapture attrition curves (Kleiber et al., 1987) that plotted the number of tagged fish recaptured against time at liberty. The elapsed time at which 50% of the releases had been recaptured at the point of release (Cross Seamount) represents the "half-life" of resident tuna within that area. That is, for a group of animals tagged at Cross Seamount, the residence time was defined as the elapsed time at which only half those animals remained at that location. In order to avoid disproportionate influence of fish recaptured immediately after release and be-

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Table 1
Fish tagged and released at Cross Seamount.

	Released at Cross	Recaptured at Cross		Recaptured elsewhere		Combined recaptures	
Yellowfin	458	86	(18.7%)	9	(1.9%)	95	(20.7%)
Bigeye	835	61	(7.3%)	12	(1.4%)	73	(8.7%)
Total	1293	147	(11.4%)	21	(1.6%)	168	(12.9%)

cause nighttime is when tuna often make significant horizontal movements away from their daytime haunts (Holland et al, 1990; Marsac et al., 1995), attrition curves were constructed only for fish recaptured for time at liberty >24 h.

Results

Between August 1995 and November 1996, 835 bigeye and 458 yellowfin tuna were released at Cross Seamount. The tagged bigeye tuna were between 40 and 105 cm FL; yellowfin released were between 40 and 90 cm FL. There were no significant differences between the two species in the size distribution of fish tagged and released (Fig. 2) or in size distribution of the recaptures. Because no effort was made to preferentially tag a particular species, the ratio of releases (65% bigeye, 35% yellowfin) reflected the ratio of species actually caught. Release and recapture data are summarized in Table 1.

The numbers of yellowfin and bigeye tuna recaptured at Cross Seamount were aggregated into 30-day periods of time at liberty and plotted as percentages of total number of fish recaptured. The resultant regression curves for the recapture of each species are shown in Figure 3. An analysis of covariance indicated that the slopes of the attrition curves for the two species are significantly different (P=0.013). The attrition rate (slope of the regression line) for yellowfin tuna is approximately twice the rate for bigeye tuna, and the slopes indicate a residence time (50% recaptured) of 15 days for yellowfin tuna and 32 days for bigeye tuna. By contrast, the tag attrition

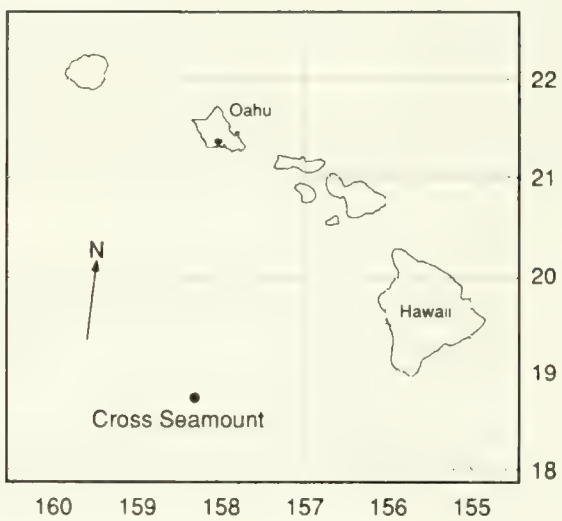

Figure 1
Chart of the study area showing position of Cross Seamount in relation to the main Hawaiian Islands.

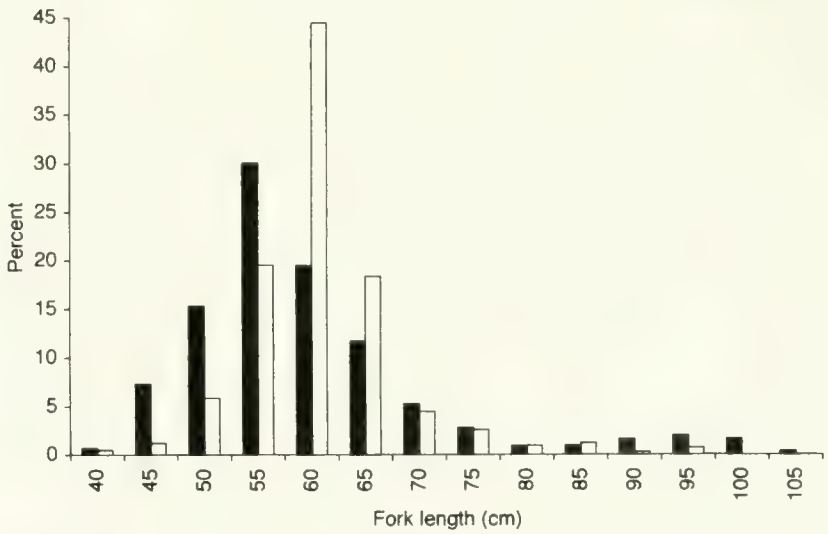

Figure 2
Size distribution of bigeye tuna and yellowfin tuna tagged and released at Cross Seamount. Solid bars = bigeye tuna; open bars = yellowfin tuna.

curves for statewide returns (that is, time at liberty for all recaptured Cross Seamount yellowfin and bigeye tuna, regardless of recapture location) were not significantly different (P=0.45, Fig. 3).

In addition, there were more recaptures of bigeye tuna with longer periods at liberty than of yellowfin tuna at the seamount and the longest time at liberty was 169 days for bigeye tuna compared with the longest point-of-release recapture of 93 days for yellowfin tuna.

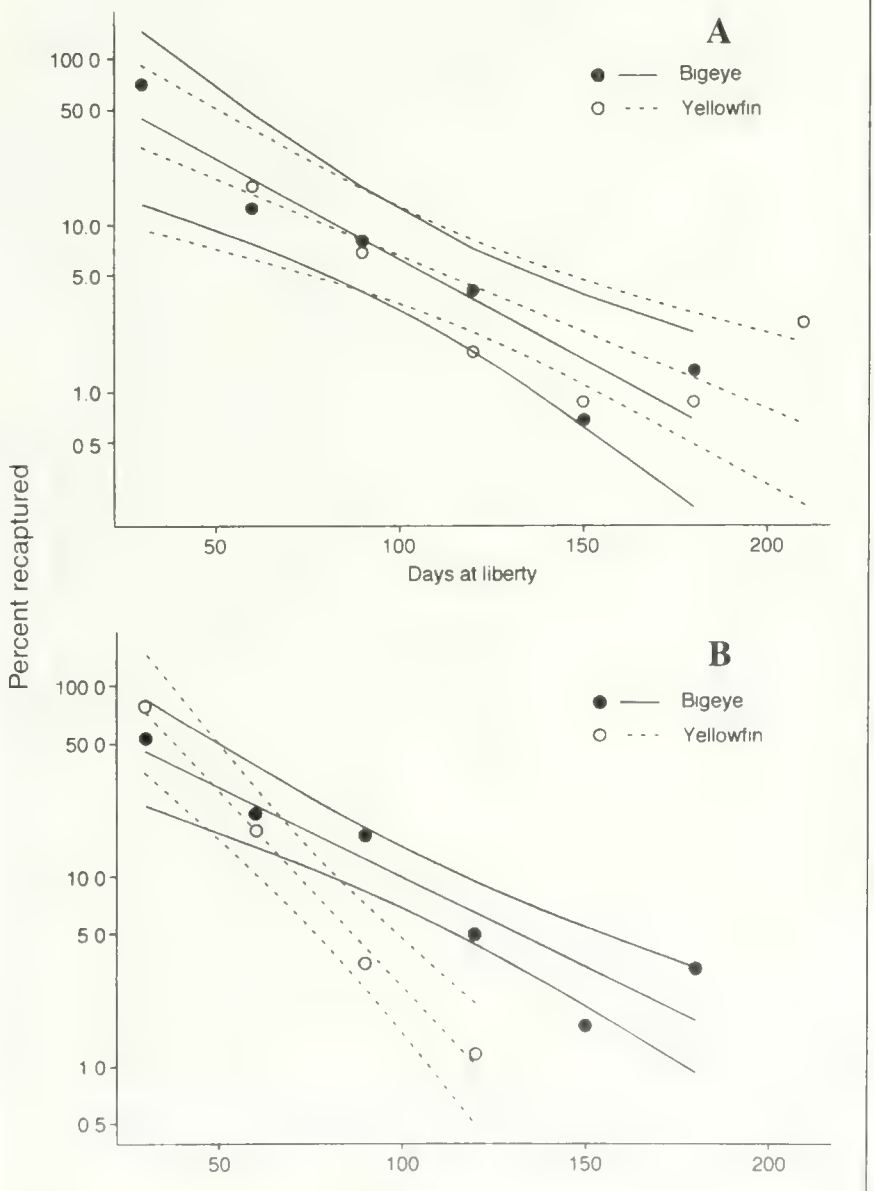

Figure 3

Tag recapture attrition curves (semi-log plots with 95% confidence contours) for bigeye and yellowfin tuna tagged and released at Cross Seamount. **(A)** All recaptures from all locations; **(B)** Recaptured at Cross Seamount.

Discussion

The main thrust of this analysis was to compare the residence times of the two tuna species at Cross Seamount. Consequently, many complicating factors often associated with analysis of tag-and-recapture data could be avoided (especially the impact of variability of fishing effort on the temporal pattern of recaptures) because effort could be assumed to be equal for both species. Therefore, the difference in the tag attrition curves, and the resultant difference in residence times ("half-life"), probably reflect real differences in the behavior of these two species at Cross Seamount. The similarity of the recapture curves for the entire area (Fig. 3) further suggests that methodological or experimental biases are not responsible for the differences in attrition curves obtained for these two species at Cross Seamount.

These results differ from those of Fonteneau (1991) who observed no differences in the temporal characteristics of recaptures of tagged bigeye, yellowfin, and skipjack tunas released at a seamount in the tropical Atlantic.

Fisheries data (Hanamoto, 1976, 1987) and acoustic tracking (Holland et al., 1990) both indicate that the open ocean behavior of bigeye and yellowfin tuna is different. Bigeye tuna select colder waters and are therefore usually found deeper than yellowfin tuna, which orient principally to the top of the thermocline and the mixed surface layer. However, this vertical separation breaks down around fish aggregating devices (FADs, Holland et al., 1990) and floating objects where bigeye tuna move closer to the surface and overlap in vertical distribution with yellowfin tuna. This same effect occurs at Cross Seamount where both species are caught in surface schools and bigeye tuna outnumber yellow-

fin tuna in the fishery. Similarly, mixed aggregations of yellowfin tuna, bigeye tuna, and skipjack tuna have been reported at seamounts in the Atlantic (Fonteneau, 1991).

Although the vertical behavior of yellowfin and bigeye tuna seems to merge at Cross Seamount, the current data indicate that the duration of horizontal orientation to the seamount (as measured by residence time ["half-life"]) is different.

The underlying advantage of seamounts to tuna biology is not well understood. Although seamounts can cause geographically stable regions of planktonic enrichment, it is not known if this enrichment persists long enough to move through the trophic chain to the level of the tuna forage base (Boehlert and Genin, 1987). We do know that Cross Seamount is situated in a very dynamic part of the ocean characterized by vortices created on the downcurrent side of the main Hawaiian islands (Flament et al.[1]). As these eddies spin off from the islands, current direction over the seamount can change frequently.

If an enriched area of prey does exist, and feeding is the principal underlying reason for tuna aggregations, it is difficult to understand why residence times are different for the two species and quite brief for both. The feeding advantage should impact both species equally and their residence times at the seamount should be similar. A comparison of the stomach contents of the two species when caught in seamount aggregations would be instructive. It is possible that, rather than acting as feeding stations, seamounts act as orientation points in the larger-scale movement patterns of these fish. Even though they may be too deep for visual detection, seamounts may be recognized by tuna through their ability to detect the effect of seamounts on the earth's magnetic field (Walker, 1984; Walker et al., 1984; Klimley et al., 1988). The seamounts may act as midocean reference points that may also occasionally harbor increased prey densities, the periodicity and persistence of which are driven by events in the surrounding oceanographic conditions.

A navigational role might explain why remote seamounts aggregate more tuna than seamounts located closer to land masses (Fonteneau, 1991) and why, in our study, the residence times were quite brief for both yellowfin and bigeye tuna species. The differences in the duration of orientation to the seamount might be explained if the navigational importance of seamounts is different in the broader behavioral repertoires of the two species.

Certainly, the current data indicate that Cross Seamount hosts transient populations of both tuna species rather than long-term populations. This brevity of residence at the seamount for both species probably reduces the chances of excessive fishing exploitation.

Acknowledgments

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Accuracy of at-sea commercial size grading of tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in the Australian northern prawn fishery

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The size-frequency distribution of the commercial catch is often used as the basis of fisheries stock assessments (Pauly and Morgan, 1987; Gulland and Rosenberg, 1992) because most dynamic processes of populations (growth, survival, recruitment) are reflected in changes in this distribution. The data are generally collected, often at great expense, by sampling the catch at landing sites and markets, or onboard fishing vessels.

Size-frequency distributions of prawns (*Penaeus esculentus* and *P. semisulcatus*) can also be obtained from fish processors, who grade landings by size. These data are easier and cheaper to obtain than research samples, but unfortunately they are also considered less accurate and lack spatial information. However, they have been used in stock assessment of prawns in Kuwait (Jones and van Zalinge, 1981) and Malaysia (Simpson and Kong, 1978).

It is often difficult to relate size data obtained from a processor to time and place of capture of the prawns, but this is not the case when the product is packed onboard, as in Australia's northern prawn fishery (NPF).

Trawler operators in the NPF have voluntarily recorded size composition since 1985, when provision for this was made in operators' daily logbooks (between 30% and 45% of the tiger prawn catch reported in the logbooks contain size information). These books are therefore the most comprehensive source of information on the spatial and temporal size distribution of the commercial catch of the NPF. Present assessments of the fishery are based on deterministic growth and deterministic seasonal recruitment patterns (Wang and Die, 1996) and do not use size-structured data. If available, these data would help relax the assumption of deterministic recruitment and improve current stock assessments of the NPF.

Before the size data recorded in the logbooks can be used, however, the accuracy of size grading at sea needs to be assessed. This paper examines the accuracy of grading tiger prawns, by using data collected from a private firm, A. Raptis and Sons, that operates a large modern processing factory that regularly assesses the onboard grading of product purchased from NPF trawler operators.

Although the work presented here relates specifically to the NPF, the practice of onboard size grading is widespread in other fisheries around the world. Therefore our methods have potential application to other fisheries.

Methods

At-sea commercial grading procedures

Prawns landed from the NPF are size-graded at sea because both the demand and price structure differ for prawns of different sizes. Commercial sizes are based on the number of prawns of the same size per unit of weight (per pound), and the sizes are then grouped in a range to constitute a commercial grade. For example, "9 to 12 grade" means prawns in a range of sizes individually equivalent to between 9 and 12 per pound.

The size grades (especially for the larger sizes) used for tiger prawns are often more precise than those used for other species, and the grades selected by fishermen at sea vary with operator, pack size, and target market. For this project we examined the data for the two pack sizes that were most commonly used during 1993 and 1994: small packs (3 kg) and large, variable weight (12–15 kg) packs.

Small packs Since the early 1990s, the use of accurate digital scales on many vessels has improved the accuracy of procedures for packing prawns into 3-kg or smaller packs, as well as into more conventional larger packs. The sensitivity of

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these digital scales also makes it possible to pack in more precise grades of prawns.

Prawns for these small packs are initially sorted by eye by experienced crew, and many are verified by individual weighing. Those prawns that fall outside a particular size grade are removed and the remainder are graded according to corresponding count-per-unit-of-weight tables.

Large packs Prawns for onboard grading into the large packs are sorted by eye into groups of about the same size (occasionally by counting the number into a unit of weight [often a pound measured on analogue scales] and grouping them accordingly). Very large and very small prawns are removed and regraded.

Quality control assessment in the factory—source of data for analysis

A. Raptis and Sons process tiger prawns caught by their own large fleet of trawlers working in the NPF, as well as prawns purchased from other fishermen operating in the same area. The company randomly checks the quality of the packs entering its factory, including the accuracy of the grading.

Packs for quality-control assessment were selected at random for every vessel and from all consignments entering the factory. All packs were clearly marked with the vessel's name, the prawn species group, the grade of the prawns, and the date caught.

The selected samples were thawed individually. For the small packs, net weight was recorded, and size grading was checked by counting all prawns from each pack and averaging the count. Large and small prawns that did not fit the grade category were selected by eye, weighed, and graded individually, and the percentage by weight and the true grade of these prawns were recorded along with the percentage of those correctly graded.

With the large packs, a variable 2.5–3 kilogram sample of prawns was randomly taken from each pack, counted, and checked as above. The percentage by weight and the true grade of incorrectly graded prawns in the sample were recorded.

Categorical analysis

The results of all factory quality-control checks on both the small and large packs between mid-1993 and the end of 1994 were examined. Over this time, samples from 51 of the 127 boats that fished different areas in the NPF had been taken. We split the data into three time periods to find out whether the accuracy of grading early in the year differed from grading that took place later in the year when smaller prawns recruited to the fishery. Period one was from July to December 1993, period two from January to June 1994, and period three from July to December 1994.

Table 1

Commercial size grades (*) used in grading and quality-control assessments of tiger prawns for two different pack sizes. Also shown are the ranges of carapace lengths (mm) for each size grade.

Grade (prawn count (per lb)	Carapace length (mm)	Small pack	Large pack	Quality control
Under 6	>46	*	*	*
6 to 8	46–42	*	*	*
Under 10	>39		*	
9 to 12	41–36	*	*	*
10 to 15	38–33		*	
13 to 15	35–33	*	*	*
16 to 20	32–30	*	*	*
10 to 20	38–30		*	
Over 20	<29	*		
21 to 25	29–28		*	
26 to 30	27–26		*	
21 to 30	29–26		*	*

Data from the large packs, where the grades used were not the same as those for the small packs, were omitted from the analysis because they could not be compared directly. The commonly used size grades for both pack sizes are shown in Table 1, as well as the equivalent carapace length of the prawns.

The number of prawns (n) contained in the small packs was recovered by converting the net weight of the pack to pounds (weight in kilograms divided by 0.45359), and then by multiplying by the count-per-pound derived from the quality-control inspection. The number of misgraded prawns (r) in the small packs was estimated by multiplying the number of prawns in the sample by the percentage misgraded in that pack. The numbers misgraded for each period and each size grade were analyzed by fitting binary regression models by means of iterative weighted least squares. The number of misgraded prawns was assumed to have a binomial distribution:

$$Pr = \binom{n}{r} \pi^r (1-\pi)^{n-r}, \qquad (r=0, 1...n)$$

with P(misgraded) = π and P(correctly graded) = $1 - \pi$. The probability π was modelled in terms of the log-odds or logistic transformation ($\log(\pi/(1 - \pi))$. The computed deviance statistic, approximately distributed as chi-squared, was used in goodness-of-fit tests.

It was not possible to recover the total number of prawns in the large packs because the variable sample weight (between 2.5 and 3 kilograms) was not recorded in the Raptis database. Therefore estimates of the number of misgraded prawns were derived only for the samples and not for the whole pack. Because these samples were randomly chosen, it was possible to assume that the assessment of grading accuracy was representative of the grading accuracy for the whole pack.

For the large pack samples, the proportion misgraded had a mean (Eq. 1) and variance (Eq. 2) over the different samples

$$\text{Mean} = \pi \tag{1}$$

and

$$Variance = E\left(\frac{\pi(1-\pi)}{n}\right), \tag{2}$$

where π = the misgrading probability; and
n = the sample size.

Because the weight range of the samples was small, it was possible to estimate the expected reciprocal sample size

$$\left(E\left(\frac{1}{n}\right)\right)$$

(Eq. 4) by integrating over the sample weight range (assumed for mathematical convience to be uniformly distributed between 2.5 kg and 3 kg) (Eq. 3):

$$E\left(\frac{1}{n}\right) = \int_{2.5}^{3} \frac{0.45359}{\rho w} 2dw \tag{3}$$

$$= \left(\frac{0.45359 \times 2 \times \ln(3/2.5)}{\rho}\right) \tag{4}$$

where ρ = count per pound;
0.45359 kg = 1 lb; and
w = sample weight.

The relationship between Equations 1 and 2 here is the same as that for the binomial distribution; therefore the data were analyzed by fitting binomial regression models.

The size of misgraded prawns was examined to determine whether misgrading was a result of including small prawns in large grades or vice versa. The number of size grades in which misgrading occurred was also assessed.

Results

Small packs

Of the 21,443 tiger prawns in 293 small packs that were assessed, an estimated 1937 (9%) prawns in 229 packs were misgraded. There were significant changes in the proportion misgraded with both period of catch and size grade, with higher proportions of misgraded prawns in the small size grades (Table 2; Fig. 1A). Overall, grading accuracy tended to increase over the 18 months examined (Fig. 1A).

The size of the misgraded prawns over the different grades did not show a consistent pattern, but generally larger prawn grade packs tended to contain smaller prawns (Fig. 1A). The proportion of misgraded prawns that should have been in smaller grades, however, was

1 not constant over all size grades within each period of catch (Table 3; Fig. 1A);
2 not the same for each size grade over the three periods examined (Table 4; Fig. 1A).

Of the misgraded prawns, 99% were size-graded either one grade larger or one grade smaller. Only grades 9 to 12 and 16 to 20 contained prawns misgraded by as much as two size grades, with no more than 2% so misgraded. Because there was no larger grade, prawns misgraded in the under 6 size, were graded as 6 to 8.

If the proportion of prawns graded size i by fishermen at-sea that were actually size j (i, j=1 for under 6, 2 for 6 to 8, 3 for 9 to 12, 4 for 13 to 15, 5 for 16 to 20, and 6 for over 20 prawns per pound) obtained from the sample data are denoted by θ_{ij}, then the proportions, p_i, of all prawns graded as size i at-sea can be adjusted with the equation:

$$\sum_{i=1}^{5} p_i \theta_{ij} \tag{5}$$

to give a corrected grade size distribution (j=1, 2, ..., 6). Shown in Table 5 are the corrected distributions compared with at-sea grading for the small packs. The adjustments can be seen to be quite modest, and the at-sea gradings provide a reliable assessment of the size distribution.

Large packs

Samples containing an estimated 8210 tiger prawns from 124 large packs were assessed. Of these samples, an estimated 2914 (35%) prawns from 107 packs were misgraded. Again, there were significant

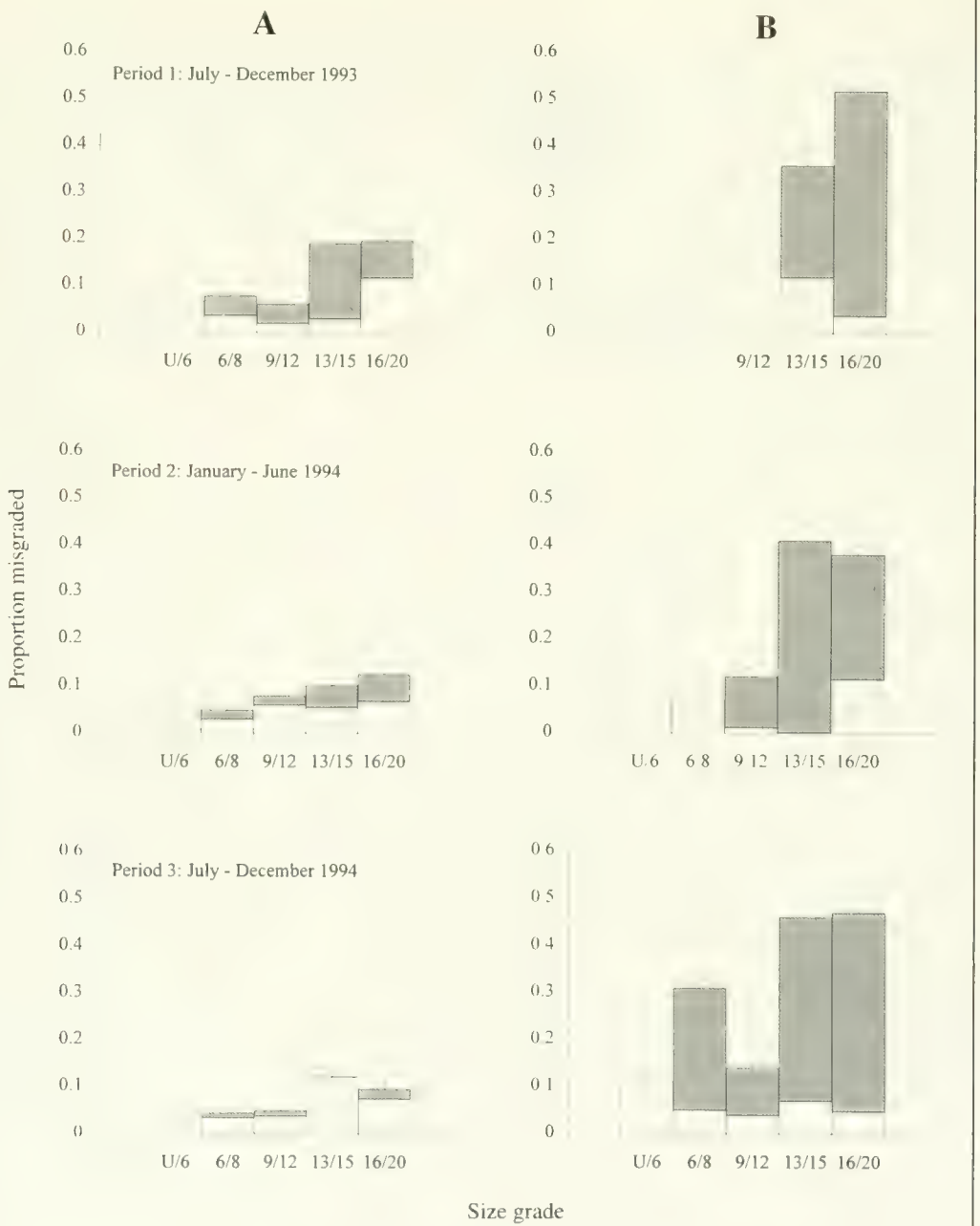

Figure 1

The proportion (+SE) of misgraded tiger prawns from each size grade, for (**A**) the small packs and (**B**) the large packs. The proportion misgraded was split between prawns that were misgraded too large (white) and those that were misgraded too small (gray).

changes in the proportion misgraded with period of catch and size grade, with significant differences in the proportion misgraded with period of catch, and generally higher proportions of the smaller size grades misgraded (Table 2; Fig. 1B).

There was a tendency for smaller-prawn grade packs to contain larger prawns (Fig. 1B). The proportion of misgraded prawns that should have been in a larger-size grade, however, was

1 not constant over all size grades, within any one period of catch (Table 3; Fig. 1B);
2 not the same for each size grade, over the three periods examined (Table 4; Fig. 1B).

Table 2

Binomial model fits for each period of catch (1: July–December 1993, 2: January–June 1994, and 3: July–December 1994) and pack-size combination. (a, b, c) denote groups of size grades with no significant differences in the proportion of misgraded prawns.

Pack size	Time period	Size grade					χ^2	df	P
		Under 6	6 to 8	9 to 12	13 to 15	16 to 20			
Small		a	a	a					
	1				b	b	1.517	3	0.68
		a	a						
	2			b			0.476	1	0.52
					c	c			
		a							
	3		b	b			3.244	2	0.20
					c	c			
Large				a					
	1				b		[1]		
						c			
			a	a					
	2	b			b	b	2.695	3	0.44
		a		a					
	3		b				2.892	2	0.24
					c	c			

[1] Zero degrees of freedom.

Table 3

Chi-squared statistics for the constant model of misgraded prawn size in each period of catch (1: July–December 1993, 2: January–June 1994, and 3: July–December 1994), for both small and large packs. * $P< 0.0001$

Period	Small pack	Large pack
1	45.088	17.963
2	45.916	55.701
3	32.915	83.060

Table 4

Chi-squared statistics for the constant model of misgraded prawn size in each size grade for both small and large packs. *$P< 0.0001$, **$P= 0.13$, ***$P= 0.03$.

Size grade	Small pack	Large pack
6 to 8	4.1494 **	14.408 *
9 to 12	33.271	4.7639 ***
13 to 15	220.58	27.039
16 to 20	16.159	106.83

Of the prawns misgraded, 92% were sized either one grade larger or smaller. Of those misgraded in the 16 to 20 grade, 11% were misgraded by as much as two grades, whereas less than 2% were so misgraded for the other size grades.

The misgrading proportions can again be used in Equation 5 to obtain the at-sea grade-size distribution for these large packs. Shown in Table 5 are these corrected distributions compared with at-sea gradings; here the adjustments can be seen to be more substantial than those for the small packs, particularly for the smaller grades 13 to 15 and 16 to 20 prawns per pound, owing to the tendency of the fishermen to classify the prawns to smaller size grades.

Discussion

Our analysis indicates that small prawns are graded less accurately than large ones. Given that the length

Table 5

Size-grade distributions, expressed as proportions, from grading at sea and adjusted according to Equation 5.

Size grade	Period 1 (July–December 1993)		Period 2 (January–June 1994)		Period 3 (July–December 1994)	
	at-sea	adjusted	at-sea	adjusted	at-sea	adjusted
Small packs						
Under 6	0.15	0.14	0.012	0.015	0.098	0.097
6 to 8	0.16	0.17	0.19	0.19	0.11	0.11
9 to 12	0.30	0.33	0.31	0.30	0.32	0.30
13 to 15	0.26	0.23	0.28	0.28	0.24	0.23
16 to 20	0.13	0.11	0.21	0.20	0.24	0.24
Over 20	0	0.015	0	0.014	0	0.018
Large variable packs						
Under 6	—	—	0.11	0.071	0.12	0.15
6 to 8	—	—	0.059	0.11	0.17	0.15
9 to 12	0.079	0.12	0.12	0.16	0.22	0.28
13 to 15	0.055	0.43	0.10	0.22	0.14	0.21
16 to 20	0.87	0.42	0.61	0.38	0.36	0.20
Over 20	0	0.030	0	0.069	0	0.017

range corresponding to the small commercial grades is narrow (Table 1), it is perhaps not surprising that small prawns tend to be misgraded more frequently. Alternatively the grading of small prawns may be less accurate because they are less valuable than large prawns and therefore less time is spent on grading each individual.

In small packs, misgraded prawns were generally graded into larger categories, whereas in large packs, those misgraded were generally placed into smaller categories.

Incorrectly graded prawns from both pack sizes, however, tend to be incorrectly graded by only one size category, so that all prawns were graded to within three and six millimeters carapace length of their corresponding size grade.

The high proportion of landings graded and the accuracy of some of this grading suggest that size information contained in the NPF logbooks could be valuable for stock assessment. Most prawns sold in small (3-kg) packs have been accurately graded by fishermen, and these gradings could be used as a reasonable measure of the length-frequency distribution of the prawns. However, prawns sold in larger (12–15 kg) packs are graded less accurately, especially for the smaller grade sizes, and it is recommended that data from quality inspections be used to correct fishermen's grade-size distribution.

Although the work outlined in this paper was done for the Australian northern prawn fishery, similar analyses using similar methods could be carried out for other fisheries if comparable data on size gradings were available.

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Digestive tract parasites in rhynchoteuthion squid paralarvae, particularly in *Illex argentinus* (Cephalopoda: Ommastrephidae)

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Cephalopods play an important role in the transfer of parasites through the food web. They are second and third intermediate hosts for larval stages of digeneans, cestodes, and nematodes. The final hosts are usually fishes, sea birds, and marine mammals (Hochberg, 1990). Nevertheless, the interactions of cephalopods and their parasites are still poorly understood, and almost nothing is know about parasitism in cephalopod paralarvae and early juveniles (Vecchione, 1987). Information on parasitism in the early stages of cephalopod life cycles can provide a better understanding of host-parasite relationships as well as the environment and conditions in which infection first occurs.

Ommastrephid paralarvae are among the smallest cephalopods at hatching and are termed "rhynchoteuthion" because their tentacles are fused into a proboscis-like structure. Three distinct morphological types of rhynchoteuthion paralarvae (types "A," "B," and "C") are found commonly off southern Brazil (Haimovici et al., 1995). "Type C" is *Illex argentinus* (Castellanos, 1960) and "type A" probably is *Ommastrephes bartramii* (Lesueur, 1821). *Illex argentinus* is distributed in the southwestern Atlantic Ocean from 22° to 54°S (Roper et al., 1984), and it currently supports the largest squid fishery in the world. This species is an important link in the trophic relations of the pelagic ecosystem of this region and constitutes a major element of the diet of several commercial fishes, such as *Thunnus obesus*, *Merluccius hubbsi*, *Xiphias gladius*, and *Polyprion americanus* (Santos, 1992; Ivanovic and Brunetti, 1994).

The digestive tract contents of *Illex argentinus* and the other rhynchoteuthion types were examined by Vidal and Haimovici (1998). During examination of the digestive tracts, observations on parasitism were made. In this note we report the parasites (protistans and metazoans) found in the digestive tract of rhynchoteuthion paralarvae, mainly *Illex argentinus*.

Material and methods

Ommastrephid paralarvae were collected in four surveys carried out between Cape of Santa Marta Grande (28°30'S) and Chuí (34°20'S), Brazil, during the spring of 1987, summer of 1990, autumn of 1991, and winter of 1988. Paired bongo nets, with 60-cm mouth diameter and 0.33-mm mesh were used in oblique tows between the surface and depths of approximately 300 m. This gear was towed at a speed of 2 kn and deployed for 5–15 min. Afterwards, paralarvae were fixed and preserved in formalin.

Digestive tracts were examined from paralarvae of 72 *I. argentinus* (1.0–8.0 mm of mantle length (ML)), 12 "type A" (1.0–5.8 mm ML) and 4 "type B" (2.0–4.0 mm ML). Paralarvae were stained with alcian blue and then cleared with trypsin, following the method of Vecchione (1991). This method makes the paralarvae semitransparent and the parasites in the gut easier to see. The stomach, caecum, and intestine of all paralarvae were examined for parasites with a light microscope at a magnification of 400×. The esophagus was not examined. Five *I. argentinus* juveniles (16.0–38.0 mm ML) and 14 paralarvae (1.6–9.7 mm ML) of *I. argentinus* with no previous clearing and staining treatment were also examined. The prevalence and the mean intensity of infestation (number of a particular parasite per infected individuals) were calculated according to Margolis et al. (1982).

Results

Parasites were not found in the 14 untreated paralarvae. The opaque walls of the internal organs made the visualization of parasites difficult. A single copepod parasite was found in one of the five untreated juveniles.

Four types of parasites were observed in paralarvae and juvenile *I. argentinus*: coccidians (Apicomplexa: Sporozoea: Eucoccidiida), didymozoid-metacercariae (Platyhelminthes: Trematoda: Digenea),

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Table 1

Results of examinations of rhynchoteuthion paralarvae from four surveys conducted between the spring of 1987 and autumn of 1991. + = presence; 0 = absence.

	Spring 1987		Summer 1990	Autumn 1991		Winter 1988
	Illex argentinus	"Type B"	"Type A"	*Illex argentinus*	"Type B"	*Illex argentinus*
Paralarvae mantle length (mm)	1.0–8.0	2.8	1.0–5.8	1.3–5.5	2.0–4.0	1.0–7.8
Digestive tracts examined	41	1	12	19	3	12
Parasites:						
Nematode	+	0	0	0	0	0
Aggregata sp. (coccidian)	0	0	0	0	0	+
Didymozoids						
Monilicaecum sp.	+	0	+	+	0	+
Prevalence (%)	7.3		72.0	10.5		8.3
Mean intensity of infestation	2.3		3.5	1.5		1.0

a nematode (Nematoda) and a copepod (Arthropoda: Crustacea: Siphonostomatoida). About 50 coccidians (*Aggregata* sp.) were found distributed along the caecum wall of a 7.8-mm-ML paralarva collected in winter. Because the paralarva was preserved in glycerin for several months, taxonomic details of the parasites were not very clear. Cyst capsules (sporocystes) varied in size from 11 to 17 µm. However, the detailed structures inside the capsules were obscure and no certainty could be attained about the presence of sporozooites; hence this protozoan was assigned to the genus *Aggregata*. The observed parasites may have been in a very early stage of development and if the capsules actually represent sporocystes they were unusual because only 1 or 2 were present inside an amorphous oocyst mass (Hochberg[1]). These parasites are deposited at the Santa Barbara Museum of Natural History.

Six *I. argentinus* paralarvae (2.2–6.7 mm ML) from autumn, winter, and spring surveys contained 1–3 didymozoid metacercariae, probably type *Monilicaecum*. The body dimensions of the parasites ranged from 140 to 200 µm and because of their size and the absence of testicular anlagen, they appeared to be recently hatched. A single trematode attached to the caecum wall was found in the smallest paralarva. Three parasites were found in the largest paralarva, two attached to the stomach wall and one near the buccal mass. In the other paralarvae, the parasites were found attached to the caecum wall. Data on prevalence and mean intensity of infestation of different paralarval types and surveys of didymozoids are presented in Table 1. We found a single (nematode attached to the caecum wall of a 7.0-mm-ML rhynchoteuthion from the spring sample. The copepod parasite was located on the caecum wall of a 38.0-mm-ML juvenile obtained in spring. The copepod was identified as an adult male of *Metacaligus uruguayensis* (Siphonostomatoida: Caligidae) (Ho and Bashirullah, 1977). *Illex argentinus* is a newly recorded host for *M. uruguayensis*.

In the summer of 1990, didymozoid metacercariae were found in "type A" rhynchoteuthions from 2.0 to 5.0 mm ML. Prevalence was 72% and the mean intensity of infestation was 3.5 (Table 1). All were attached to the caecum or stomach walls, except for three parasites attached to the inner wall of the mantle and two others to the caecum wall of a single paralarva (3.6 mm ML).

Parasites were not found in "type B" rhynchoteuthions. However, only four paralarvae of this type were examined.

Discussion

Illex argentinus first acquire didymozoid metacercariae as small rhynchoteuthions. Hatchlings typically are found off southern Brazil at the outer shelf and slope in tropical and subtropical waters (Vidal and Haimovici, 1997). The infestation may be related to the fact that paralarvae are distributed mainly in tropical waters, where cystophorous cercariae may be abundant and not necessarily because the paralarvae are eating infected intermediate hosts. Crustacean prey were not found in the digestive tracts of rhynchoteuthions smaller than 3.7 mm ML (Vidal and Haimovici, 1998). However, paralarvae

[1] Hochberg, F. G. 1997. Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Personal commun.

larger than this size could also be infested by consuming infected second-intermediate hosts, such as copepods and other crustaceans.

Infestation in the smaller rhynchoteuthions may occur when free cystophorous cercariae are released into the plankton and passively enter the mantle cavity during respiration (Gaevskaya, 1976) or when the cercariae attach to mucus that covers the mantle and head of rhynchoteuthions. They may also be ingested directly, in the same way that crustaceans are infested. If this is true, ommastrephid paralarvae may act as second intermediate hosts for some didymozoids. The presence of didymozoid metacercariae in the digestive tracts of rhynchoteuthions as small as 2.0 mm ML shows that the infection occurs well before that previously recorded by Gaevskaya and Nigmatullin (1983). Additionally, the size of the didymozoid metacercariae type *Monilicaecum* (140–200 μm) found on rhynchoteuthion paralarvae is strong evidence that they are in an early developmental stage in relation to those found on adult *I. argentinus* from southern Brazil (400–800 μm) (Santos, 1992). Our results are in accordance with the suggestion of Hochberg (1990) that didymozoids can grow inside the squid host. Hochberg (1990) also reported that a peak of infestation by didymozoids occurs in squids from 10 to 25 cm in ML. Nevertheless, infection decreases in adult individuals (Gaevskaya and Nigmatullin, 1977, 1983) owing to the fact that the didymozoids die after they reach a maximum size in a specific host (Hochberg, 1990). Larger squids may be reinfected by didymozoid metacercariae when they feed on infested fish prey (Hochberg, 1990). Our results indicate that more paralarvae should be examined in the future. If it is correct to assume that recently hatched didymozoid metacercariae usually infest early paralarvae, information on size and developmental stage of both host and parasites would help to understand their relationship better.

Didymozoid metacercariae were found in *I. argentinus* rhynchoteuthions from autumn to spring and in "type A" rhynchoteuthions during the summer. This morphotype had a higher prevalence and infestation of didymozoids than those of *I. argentinus*. They were collected in the summer of 1990, when tropical waters dominate the study area (Vidal and Haimovici, 1997). Thus, these larval trematodes are present off southern Brazil throughout the year. This finding is in agreement with the occurrence of the high prevalence and intensities of didymozoid metacercariae in juvenile and immature *I. argentinus* from the same area year around (Santos, 1992).

Only the sexual stages of *Aggregata* occur in cephalopods, whereas asexual stages infect the digestive tracts of crustaceans (Hochberg, 1990). *Aggregata* appears to be host-specific only in cephalopods, not in crustaceans, and is a common parasite of *Sepia* and *Octopus* (Hochberg, 1990). Our study is the first to report its presence in *I. argentinus*. This coccidian has not been found in adults of *I. argentinus* collected off southern Brazil (Santos, 1992) or Argentina (Nigmatullin and Shukhgalter, 1990; Sardella et al., 1990). *Martialia hyadesi*, a southern Atlantic oceanic species, and *Todaropsis eblanae* and *Todarodes sagittatus* in waters off Spain are the other ommastrephid squids in which *Aggregata* have been reported (Gaevskaya et al. 1986, Pascual et al. 1996). It is important to stress that infections by *Aggregata* can only be established after paralarvae begin to feed on crustaceans infected with the asexual stages of the parasite. The infected paralarva observed in this study was 7.8 mm ML; however, crustacean prey, mainly copepods, have been found in the gut of *I. argentinus* paralarvae larger than 3.7 mm ML (Vidal and Haimovici, 1998).

Metacaligus uruguayensis was originally described from the gill cavity of *Trichiurus lepturus* from Venezuela (Ho and Bashirullah, 1977). This genus previously has not been reported from cephalopods (see review by Hochberg, 1990). Associations between copepods and cephalopods appear to be primarily commensal and not truly parasitic (Hochberg, 1990). In southern Brazil, small and large adult *T. lepturus* (70–1000 mm TL) occasionally prey on juvenile and adult *I. argentinus* (22–200 mm ML) (Martins, 1992); however, additional information is required to determine whether *I. argentinus* serves as a final or only an accidental host for this copepod.

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Diet of Pacific sleeper shark, *Somniosus pacificus*, in the Gulf of Alaska

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The sleeper shark, *Somniosus pacificus*, ranges from Chile (Crovetto et al., 1992) through southern California (Phillips,1953), British Columbia to the Gulf of Alaska (Bright,1959), the Bering Sea (Wilimovsky,1954), and Japan (Tanaka et al.,1982). It is thought to be a voracious and versatile feeder and its diet has been shown to include young marine mammals, such as harbor seal, *Phoca vitulina* (Bright,1959), and the southern right whale dolphin, *Lissodelphis peronii*, (Crovetto et al.,1992). The purpose of this study is to describe the diet of the sleeper shark in the Gulf of Alaska area.

Methods

Sleeper sharks were collected in the Gulf of Alaska (Fig. 1) between June and August 1996 from the longline vessel *Alaska Leader*, and the bottom-trawl vessels *Vesteraalen* and *American No. 1*. After dissections onboard, each individual stomach was put in a plastic bag and frozen at sea. Tags recording date, location, and length and sex of shark were included in the sample bag. Information on the station, shark total length (TL) (measurements follow Castro, 1983), and dates samples were collected are listed in Table 1. Stomachs were thawed in the laboratory and stomach contents were analyzed. Prey were identified to the lowest taxonomic level possible. Each prey item was weighed and standard length of prey fish was measured. Percent frequency of occurrence and the percentage of the total weight of each prey item were calculated. Octopus beak measurements were made to estimate live wet weights of octopi. According to Robinson and Hartwick (1983), pigment-upper-lateral-wall length (PULWL) has the best correlation coefficient with the live wet weight of the North Pacific giant octopus, *Octopus dofleini*; we therefore used these PULWLs to estimate the live wet weight of the octopus. Live wet weights of *Octopus dofleini* that had been consumed were calculated by using Robinson and Hartwick's (1983) equation:

$$\ln(PULWL(\text{mm})) = 0.274 \ln(weight(\text{kg})) + 2.674. \quad (1)$$

Results

A total of 13 sleeper shark stomachs were analyzed; two were empty, 11 contained food (Tables 1 and 2). The length of the sleeper sharks ranged from 218 cm to 295 cm TL (mean= 264.5 cm; SD=24.9 cm. Arrowtooth flounder, *Atheresthes stomias*, was the most important prey, representing 67% of the total stomach content weight (64% of frequency of occurrence). The size of arrowtooth flounder consumed by sleeper sharks ranged from 38 cm to 65 cm TL, (mean=44.8 cm; SD=8.0 cm). Other prey included a 48-cm walleye pollock, *Theragra chalcogramma* (5.2% by weight), a single 33-cm rockfish, *Sebastes* sp., a 40-cm Pacific salmon, *Oncorhynchus* sp., and a 26-cm flathead sole, *Hippoglossoides elassodon*, as well as three unidentifiable flatfish. *Octopus dofleini* were the most important invertebrate found in the diet of sleeper sharks, representing 5% of the total stomach contents weight and 73% of the frequency of occurrence. The estimated wet weight of *Octopus dofleini* (based on beak measurements) ranged from 5.65 kg to 29.07 kg (mean=18.51 kg; SD=6.58 kg). The PULWL measurements ranged from 23.3 mm to 36.5 mm (mean=31.78 mm; SD= 3.64 mm). Less important invertebrate prey included squids, snails (*Fusitriton* sp.), hermit crabs, and gammarid amphipods. Fish offal (five arrowtooth flounder heads) was found in one sleeper shark stomach. It represented 12% of the total stomach contents weight and had a frequency of occurrence of 9%. No Steller sea lion parts were found in the 13 sleeper shark stomachs examined.

In our study, three specimens were collected from bottom trawls, ten from longline surveys. The weight of stomach contents of the three specimens collected from bottom trawls (sharks no. 4, 12, and 13) were more than 2000 g (4506 g; 2321 g; and 11,782 g, respectively), whereas weight of stomach contents of the specimens collected from long lines were much lower than those collected from the bottom trawls (only three weighed more than 500 g, one weighed more than 3000 g, and the rest weighed less than 50 g). Less food in the stomachs of the sleeper sharks col-

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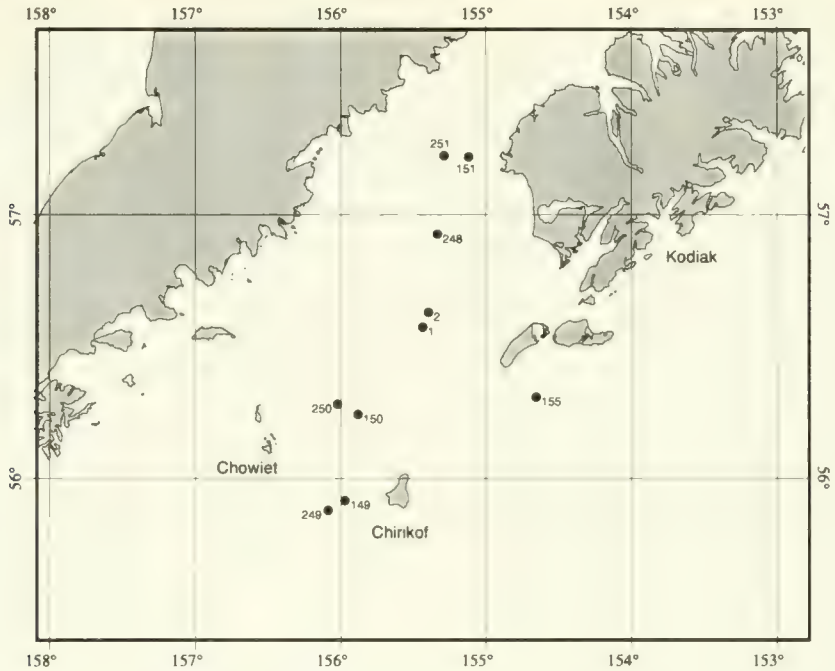

Figure 1
Locations of sleeper sharks collected in Gulf of Alaska

Table 1
Some information on the 13 sleeper shark, *Somniosus pacificus*, stomachs collected in the Gulf of Alaska in 1996. TL = Total length; Wt = stomach contents weight.

Date	Vessel	Station no.	Depth (m)	Shark no.	TL (cm)	Wt (g)
24 Jun '96	*Alaska Leader*	149	241	7	274	520
24 Jun '96	*Alaska Leader*	249	253	11	218	12
25 Jun '96	*Alaska Leader*	250	267	2	292	39
25 Jun '96	*Alaska Leader*	250	267	5	287	3094
25 Jun '96	*Alaska Leader*	250	267	6	249	0
25 Jun '96	*Alaska Leader*	150	240	8	284	821
26 Jun '96	*Alaska Leader*	151	240	1	295	0
26 Jun '96	*Alaska Leader*	151	240	3	274	11
26 Jun '96	*Alaska Leader*	251	255	9	244	11
27 Jun '96	*Alaska Leader*	248	263	10	244	900
28 Jun '96	*Vesteraalen*	155	86	4	274	4506
3 Aug '96	*American No. 1*	1	101	12	229	2321
4 Aug '96	*American No. 1*	2	113	13	274	11,782

lected by longlines is probably caused by regurgitation during the long operation (two to six hours) of longline surveys. Our data also indicate that more prey items (e.g. walleye pollock, salmon, rockfish, and snails) were found in stomachs collected by bottom trawls than collected from longlines (mainly arrowtooth flounder and octopus). Bottom depths (Table 1) for the samples collected from bottom trawls were shallower (from 86 to 113 m) than for samples collected from longlines (from 240 to 267 m); bottom depth may also be a factor in the diet variations. Length of the sleeper sharks (Table 1) might also affect their diet; owing to the small sample size, however, no comparisons could be made from our study.

Discussion

On the basis of our sampling of stomach contents, sleeper sharks appear to feed mainly on the bottom. Even though *Octopus dofleini* represented only 5% of the total stomach content weight, they occurred in a high percentage of sleeper shark stomachs (73%). Other researchers have also found that benthic fish and invertebrates are the predominate species in the diet of sleeper sharks. Phillips (1953) found a sleeper shark in California that had fed on rockfish. Gotshall and Jow (1965) found that the diet of sleeper shark included rex sole, *Glyptocephalus zachirus*; Dover sole, *Microstomus pacificus*; Pacific halibut, *Hippoglossus stenolepis*; and cephalopods.

The diet of sleeper sharks vary with their size. Gotshall and Jow (1965) described the main food of a 114-cm female sleeper shark as *Moroteuthis robusta*. In our study lengths of sleeper sharks ranged between 200 and 300 cm. Their diets consisted mainly of arrowtooth flounder, walleye pollock, and cephalopods. Larger sleeper sharks (360–400 cm) have been reported to consume not only fishes and cephalopods, but also marine mammals, i.e. harbor seal (Bright, 1959) and southern right whale (Crovetto et al., 1992).

Table 2

Prey items (expressed in percent frequency of occurrence (%FO), and percent total weight (%W)) of sleeper shark, *Somniosus pacificus*, collected in Gulf of Alaska in 1996.

Prey name	%FO	%W
Gastropod (snail)	9.09	0.49
Fusitriton sp. (snail)	9.09	0.19
Cephalopod (squid and octopus)	27.27	0.17
Teuthoidea (squid)	36.36	0.62
Octopus dofleini (octopus)	72.73	4.63
Crangonidae (shrimp)	9.09	0.01
Pagurid (hermit crab)	9.09	0.01
Teleostei (unidentified fish)	45.45	0.33
Oncorhynchus sp. (salmon)	9.09	4.49
Gadidae (gadid fish)	9.09	0.49
Theragra chalcogramma (walleye pollock)	9.09	5.22
Atheresthes stomias (arrowtooth flounder)	63.64	67.21
Sebastes sp. (rockfish)	9.09	2.06
Pleuronectid (unknown flatfish)	18.18	0.86
Hippoglossoides elassodon (flathead sole)	9.09	0.98
Fishery offal	9.09	12.27
Total prey weight (g)	24,017	
Number of stomachs with food	11	
Number of empty stomachs	2	

We would like to note that stomach samples used in our study were from the area southwest of Kodiak Island, close to Steller sea lion (*Eumetopias jubatus*) rookeries at Chowiet and Chirikof Islands, as well as near numerous sea lion haulouts (Sease et al., 1993; NMFS, 1995). However, sleeper shark attacks on pups have not been reported at any time of year and we did not find evidence of predation on sea lions in our study. We did find fish offal (five arrowtooth flounder heads) in stomach samples. Bigelow and Schroeder (1948) also reported that Greenland shark, *Somniosus microcephalus* (a similar congeneric species of sleeper shark in the Atlantic Ocean), devours carrion, such as whale meat and blubber from whaling operations. It seems that sleeper shark, like Greenland shark, is sluggish and likes to stay on the bottom, feeding opportunistically on what they encounter in the environment (including carrion and fish offal).

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Morphometric separation of annual cohorts within mid-Atlantic bluefish, *Pomatomus saltatrix*, using discriminant function analysis*

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Abstract.—Larval and tagging studies neither support nor refute the existence of two mid-Atlantic stocks of bluefish, *Pomatomus saltatrix*, one that spawns just south of Hatteras, North Carolina, in the spring, and the other off New England in the summer. Subsequent studies have suggested either a continuous spawning with two survival events, or two distinct spawning events, one in spring south of Hatteras, NC, and a second in mid-summer from Long Island to New England. Genetic studies have supported a single stock because they show the existence of a single gene pool. A stepwise linear discriminant function analysis (DFA) of morphometrics of "spring-spawned" yearling (200–400 mm) and older (>400 mm) bluefish did not classify fish by probable spawning cohort. It did, however separate the yearling fish (200–400 mm) by year class rather than geographic or seasonal spawning. Older fish (>400 mm) showed less separation because multiple (2–10) year classes were present. The DNA studies have revealed genetic homogeneity among these fish. This finding suggests that the morphological characteristics are phenotypically plastic and are influenced each year by the physical environment during spawning and the early juvenile stages.

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Fish. Bull. 97:411–420 (1999).

The question of bluefish (*Pomatomus saltatrix)* stock composition along the east coast of the United States has been of considerable interest to fisheries scientists for 30 years and has recently (since 1986) become the focus of discussion by management agencies, primarily the Atlantic States Marine Fisheries Commission (ASMFC) and Mid-Atlantic Fisheries Management Council (MAFMC) (Anonymous, 1989). The problems of managing fisheries when the stock composition and boundaries are unclear have hampered effective management of weakfish, *Cynoscion regalis*, summer flounder, *Paralichthys dentatus*, surf clam, *Spisula solidissima*, and striped bass, *Morone saxatilis* by the ASMFC or MAFMC (or both) because current management practices manage by unit (genetic) stock. Interstate management is further hampered when a unit stock exhibits differential spatial reproduction and migration patterns (e.g. weakfish, Scoles, 1990).

The stock structure of the bluefish (*Pomatomus saltatrix*) in the western mid-Atlantic region is not well understood. Lund (1961) recorded meristic counts of gill rakers along the first branchial arch of young fish and suggested that six separate stocks of bluefish occur along the western north Atlantic coast of the United States. He later suggested the occurrence of several races in this region on the basis of results of two mark-recapture studies (Beaumariage and Wittich, 1966; Lund and Maltezos, 1970). These results were not supportive of Lund's original six stock concept because they suggested that there might be a "Florida" or "South Atlantic Bight" and a "northern" or "mid-Atlantic Bight" stock. Subsequent analyses of temporal and spatial distributions of bluefish in the ichthyoplankton, and spawning times, suggested two north Atlantic stocks (Norcross et al, 1974; Kendall and Walford, 1979), in addition to a south Atlantic or Florida Stock (Collins and Stender, 1987).

Chiarella and Conover (1990), on the other hand, using back calculations of scales, demonstrated that most spawning in the north mid-Atlantic Bight (MAB) occurs during mid-summer (July) and is composed of spring-spawned fish, both of which suggest a single stock. They also found from back calculations that most yearling fish (260 mm) collected in waters along Long

* Contribution 2143 from the Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA.

Island during 1986–87 were spring-spawned. Later, McBride and Conover (1991), looking at young-of-the-year bluefish in the New York Bight during the summers of 1987 and 1988, found two discrete size groups by late summer (150 mm, 75 mm). Their otolith analyses confirmed that the fish represented both spring- and summer-spawned cohorts.

More recent larval studies (Smith et al., 1994; Hare and Cowen, 1993) suggest an alternate hypothesis, that of a continuous wave of spawning by a single stock from off Hatteras in April–May to off Cape Cod or Block Island in June–July with two survival events, one in spring and one later in the summer as a result of oceanographic conditions. These survival events may have led to the previous hypothesis of two distinct spawning events. At any rate, the genetic analyses of Graves et al. (1993), using mtDNA, have shown that progeny from both the spring and summer spawning were of the same stock, and that mid-Atlantic Bight bluefish compose a single genetic stock. The various hypotheses have been revisited by Juanes et al. (1996) in a review of global bluefish early life history.

A characterization of the seasonal movement and spawning of what was then (1977) considered the north Atlantic stocks was summarized by Wilk (1977). Before the advent of routine genetic testing, Wilk (1977) conducted a morphometric analysis of yearling fish from the North Carolina sounds and Middle Atlantic Bight to test the hypothesis that two stocks of bluefish occurred in the mid-Atlantic Bight. The preliminary data, results, and manuscript were lost in the 1984 NMFS/NOAA Sandy Hook Marine Laboratory fire. Wilk did find morphometric differences that were statistically significant (Wilk[1]). If these two geographically separate spawnings are by the same stock, as demonstrated by Graves et al. (1993), but exhibit morphological differences as suggested by Wilk, perhaps due to environmental phenotypic plasticity, then a potentially valuable tool for management exists, particularly if growth, and recruitment or harvest pressure (or both) are different. With this possibility in mind, we conducted a morphometric analysis of bluefish collected in the mid-Atlantic Bight of the U.S. east coast.

Methods

A total of 1386 bluefish, ranging in size from 93 to 888 mm TL, were collected from April 1987 through April 1990 from several locations between eastern Long Island, New York, and Beaufort, North Carolina. Samples were pooled on the basis of geography and date-year of collection (Tables 1 and 2). Most were collected from pound and gill nets, but several small fish were taken by 10.8-m (30-ft) otter trawl. The majority of fish over 600 mm TL were collected by hook and line tournament fishermen.

Twenty two morphometric measurements were recorded from the left side of the fish with a meter stick or dial calipers to the nearest millimeter. Names of morphometric variables and abbreviations are provided in Table 3. Scales were removed from under the pectoral fin of each fish, mounted on acetate sheets, and ages were determined with a microfilm reader according to the techniques of Hill and Loesch.[2]

Samples were classified by using stepwise linear discriminant function analysis (DFA) (Fisher, 1936) with SPSS software program (Norusis, 1985). An excellent introduction to the statistics of discriminant analysis is presented by Klecka (1989) in which all assumptions and shortcomings of the methods are discussed. Allometric growth can cause bias, and although it is recognized that it is impossible to remove all allometric bias, Riest (1985), in a review of transformation methods, has offered Thorpe's (1975) as among the best in this situation. Schaefer (1990) and Scoles (1990) also used this technique and found it satisfactory for removing size effects during morphometric analyses of tuna and weakfish.

Consequently, all measurements were transformed following equations taken from Thorpe (1975) where

$$\hat{\hat{Y}}_i = 10^{y}$$

$$\hat{Y}_i = \log_{10} Y_i - b(\log_{10} X_i - \log_{10} \bar{\bar{X}})$$

where $\hat{\hat{Y}}_i$ = the adjusted variable of the ith specimen;
Y_i = the variable to be transformed of the ith specimen;
b = the allometric coefficient;
X_i = a standard measure of size of the ith specimen for which fork length was used; and
$\bar{\bar{X}}$ = the grand mean of standard lengths.

A third equation, combining the first two provides

$$\mathrm{Log}_{10}\left[Y_i / \hat{\hat{Y}}_i\right] = b\mathrm{Log}_{10}\left[X_i / \bar{\bar{X}}_i\right],$$

[1] Wilk, S. 1989. Sandy Hook Marine Laboratory, National Marine Fisheries Service, NOAA, Sandy Hook, NJ. Personal commun.

[2] Hill, B., and J. Loesch. 1989. Striped bass research in Virginia: characterization of Virginia commercial fisheries. Annual Report 88-89, 22 p. Virginia Institute of Marine Science, P.O. 1346, Gloucester Point, VA 23062.

Table 1

Bluefish collection data: date, location, number of fish collected, and gear used in collection. L.I.= Long Island; L.I.S. = Long Island Sound.

Date	Location	*n*	Gear
10 Mar 1987	Hatteras, NC	8	Gill net
30 Apr 1987	Aberdeen Creek, VA	10	Gill net
30 Apr 1987	Mobjack Bay, VA	21	Gill net
17 May 1987	Chesapeake Bay, VA	32	Hook and line
14 Jul 1987	Hatteras, NC	16	Seine
8 Jul 1987	Mobjack, VA	12	Gill net
2 Oct 1987	New Jersey	11	Trawl
6 Nov 1987	Chesapeake Bay, V	44	Hook and line
12 Apr 1988	Norfolk, VA	20	Gill Net
19 Apr 1988	Rappahannock R.	19	Pound net
1 May 1988	York River, VA	10	Pound net
12 May 1988	York River, VA	1	Pound net
16 Jun 1988	Ches. Bay, VA	58	Hook and line
18 Jul 1988	Pt. Lookout, L.I.	50	Gill net
19 Jul 1988	Peconic Bay, L.I.	24	Gill net
19 Jul 1988	Montauk, L.I.	71	Hook and line
25 Jul 1988	York River, VA	26	Pound net
28 Jul 1988	Hatteras, NC	85	Pound net
3 Aug 1988	York River, VA	8	Pound net
5 Aug 1988	York River, VA	76	Pound net
5 Aug 1988	L.I.S., CT	15	Trawl
9 Sep 1988	L.I.S., CT	171	Trawl
9 Sep. 1988	Potomac R.	69	Hook and line
4 Apr 1989	Pamlico Sound	81	Various
4 Apr 1989	Oregon Inlet, NC	169	Various
15 June 1989	Reedville, VA	86	Hook and line
25 July 1989	New York, NY	51	Various
15 Aug 1989	York River, VA	103	Pound net
9 Sep 1989	Hatteras, NC	42	Pound net

which more clearly shows Y_i is an estimate of the average Y_i for an individual of fork length X_i.

Following transformation, each variable was regressed against fork length (FL). The slope of each transformed variable on FL was zero or insignificant in all cases; therefore effects of allometry were disregarded. The results were plotted for visual inspection of outliers which were removed before subsequent analyses if they were outside the range of biological possibility, and thus suggested measurement error. Consequently, two subgroups of data were developed. The first included bluefish between 200 and 400 mm fork length (yearlings), to remove young-of-the-year from the data which are in the stage of growth most likely to show allometry and to duplicate the size range used by Wilk and Walford in 1964 (Wilk, 1977). The second group included bluefish greater than 400 mm fork length.

The linear discriminant function used here is of the form

$$D = B_1X_1 + B_2X_2 + B_3X_3 + \ldots\ldots\ldots B_nX_n + C$$

and is similar to a multiple linear regression

where D = the discriminant function that characterizes each reference group;

X_n's = the independent variables (individual measurements) selected at in a stepwise fashion; and

Table 2

Discriminant function analysis sample groupings by location, year, and size category. Ches Bay = Chesapeake Bay.

Group	Year	ID number	Sample size and length range (mm, in parentheses) 200–400 mm	>400 mm
Summer Hatteras	1987	1	14 (303–382)	2 (417–441)
Summer Ches Bay	1987	2	10 (258–316)	37 (448–884)
Spring Hatteras	1987	3	—	8 (684–765)
Spring Ches Bay	1987	4	15 (325–385)	30 (801–852)
Summer Ches Bay	1988	5	11 (225–382)	106 (570–830)
Summer Long Isl.	1988	6	7 (219–395)	174 (555–811)
Spring VA Coast	1988	7	—	13 (471–731)
Spring Ches Bay	1988	8	—	26 (471–757)
Summer Ches Bay	1988	9	104 (245–291)	—
Summer Hatteras	1988	10	85 (235–321)	—
Spring Hatteras	1989	11	42 (357–398)	101 (477–784)
Summer Ches Bay	1989	12	128 (215–352)	51 (405–525)
Summer Long Isl.	1989	13	-	44 (418–734)
Summer Hatteras	1989	14	—	29 (412–516)
Spring Pamlico	1989	15	71 (357–398)	7 (402–715)
Spring Ches Bay	1990	16	26[1]	30[1]
			524 (215–398)	658 (402–884)

[1] Length data lost.

Table 3

List of morphometric measurements on bluefish. Abbreviations and name of variable are those used in text.

Abbreviation	Description
PMX	Premaxilla
MAX	Maxilla
IOB	Interorbital
POB	Postorbital
POP	Preoperculum ("cheek")
OPC	Operculum
HDP	Head depth
PCO	Pectoral fin origin
PCI	Pectoral fin insertion
PLO	Pelvic fin origin
PLI	Pelvic fin insertion
VNT	Vent
AFO	Anal fin origin
AFI	Anal fin insertion
D1O	First dorsal fin origin
D1I	First dorsal fin insertion
D2O	Second dorsal fin origin
D2I	Second dorsal fin insertion
GTH	Girth
TOL	Total length
FKL	Fork length
STL	Standard length
DSP	First and second dorsal space

B_n's = the coefficients or "unstandardized function coefficients"; and

C = a constant.

Initially we intended to follow the 1960s methods of Wilk (1977) by assigning a spring-southern and summer-northern *a priori* reference designation. We were unable however, to collect a reference group of spring- and summer-spawned yearling bluefish. From the length frequencies of the yearling fish (211–382 mm) that we collected, it appeared that all were "spring-spawned" (Chiarella and Conover, 1990). As a result we made no effort *a priori* to separate "spring- spawned" from "summer-spawned" yearling fish on the basis of scale back calculations as Chiarella and Conover (1990) had done but assumed all were spring-spawned. *A priori* assignment of reference or learning groups is often used to determine the discriminant function which is then used to classify the individuals of known origin to one or the other reference groups. If, however, more than two stocks are present, the individuals of the third stock will be "force fitted" into one of the reference groups. Rather than forcing *a priori* assignments of two groups, and to identify possible additional stocks (from the south [McBride et al. 1993]) or morphometrically distinct

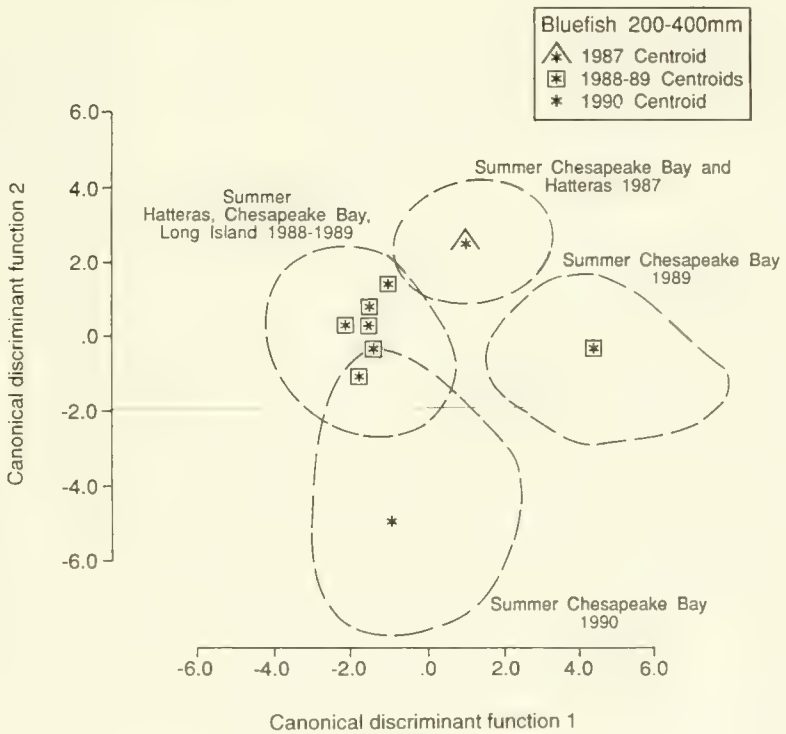

Figure 1

Scatterplot of canonical discriminant functions 1 and 2 for bluefish 200–400 mm showing locations of group centroids for 1987–90 by geographic area of collection.

groups as Wilk (1977) found, we conducted the DFA without *a priori* assignments.

Finally, an unweighted paired group method (UPGM) of clustering with arithmetic averages, a form of cluster analysis, was run to examine the relative distance between group centroids. Centroids that appear in a cluster are morphologically similar.

Results

The first five canonical functions are listed because they carry the analysis through the 95% cumulative percentage for fish 200–400 mm (Tables 4 and 5); seven functions are included for the fish >400 mm; however, the eigenvalues (Tables 5 and 6) show that only the first two functions are important in each case. The discriminant scores and centroids from functions 1 and 2 were plotted against each other to develop a graphic representation of the relationship among groups (Figs. 1 and 2).

Wilk's 1960's (1977) analysis found that the inter-dorsal space was a discriminating character. To provide a comparison, we computed an "inter-dorsal

Table 4

Summary of stepwise discriminant function analysis for 16 groups and 16 morphometric characters. Fish were 200–400 mm FL. See Table 3 for definitions of variables.

Step no.	Variable entered	Wilk's lambda	Minimum *P*	*D*	*P*
1	PLI	0.44335	<0.0001	0.00764	0.8081
2	HDP	0.34477	<0.0001	0.23817	0.2317
3	MAX	0.25160	<0.0001	0.65660	<0.0001
4	DSP	0.16585	<0.0001	0.87455	0.0001
5	IOB	0.13113	<0.0001	1.20062	<0.0001
6	OPC	0.12388	<0.0001	1.29810	<0.0001
7	PCO	0.10184	<0.0001	1.44335	<0.0001
8	AFO	0.09450	<0.0001	1.47319	<0.0001
9	D2I	0.08292	<0.0001	1.55493	<0.0001
10	D1O	0.07776	<0.0001	1.62040	<0.0001
11	AFI	0.07325	<0.0001	1.67691	<0.0001
12	POB	0.06806	<0.0001	1.69120	<0.0001
13	POP	0.06544	<0.0001	1.70979	<0.0001
14	PMX	0.05928	<0.0001	1.72065	<0.0001
15	PLO	0.05329	<0.0001	1.72103	0.0001
16	D1I	0.04386	<0.0001	1.72130	0.0001

Table 5

Summary of first five canonical discriminant functions. Fish were 200–400 mm FL.

Function	Eigenvalue	Cumulative percent	Canonical correlation	Wilk's lambda	Chi squared	df	*P*
1	2.29051	48.91	0.834324	0.15912	935.6	150	<0.0001
2	1.16710	73.84	0.733863	0.34483	541.6	126	<0.0001
3	0.54375	85.45	0.593486	0.53234	320.9	104	<0.0001
4	0.28451	91.53	0.470633	0.68379	193.5	84	<0.0001
5	0.14586	94.64	0.356785	0.78354	124.2	66	<0.0001

Table 6

Summary of the first seven canonical discriminant functions. Fish were >400 mm FL.

Function	Eigenvalue	Cumulative percent	Canonical correlation	Wilk's lambda	Chi squared	df	*P*
1	1.4858	42.4	0.77312	0.1880	1072.9	180	<0.0001
2	0.8153	65.6	0.67016	0.3413	690.1	154	<0.0001
3	0.4462	78.4	0.55546	0.4936	453.2	130	<0.0001
4	0.2595	85.8	0.45387	0.6217	305.1	108	<0.0001
5	0.1682	90.6	0.37945	0.7263	205.3	88	<0.0001
6	0.0900	93.1	0.27740	0.7917	149.9	70	<0.0001
7	0.0769	95.4	0.26722	0.8526	102.4	54	<0.0001

Table 7

Summary of stepwise discriminant function analysis for 16 groups and 16 morphometric characters. Fish were >400 mm FL. See Table 3 for definitions of variables.

Step no.	Variable entered	Wilk's lambda	Minimum *P*	Minimum *D*	Minimum *P*
1	D1I	0.7177	<0.0001	0.0007	0.9364
2	POP	0.6367	<0.0001	0.0288	0.8088
3	PLO	0.4628	<0.0001	0.2543	0.0520
4	DSP	0.4326	<0.0001	0.4455	0.1638
5	HDP	0.2946	<0.0001	0.6365	0.0008
6	AFO	0.2645	<0.0001	0.7851	0.0237
7	PCO	0.2483	<0.0001	0.8786	0.0225
8	PLI	0.1813	<0.0001	1.0243	<0.0001
9	D1O	0.1653	<0.0001	1.2288	<0.0001
10	POB	0.1323	<0.0001	1.2774	<0.0001
11	IOB	0.1090	<0.0001	1.3481	<0.0001
12	D2I	0.1025	<0.0001	1.4211	<0.0001
13	OPC	0.0994	<0.0001	1.4769	<0.0001
14	MAX	0.0996	<0.0001	1.5093	<0.0001
15	PMX	0.0776	<0.0001	1.5274	<0.0001
16	AFI	0.0756	<0.0001	1.5402	<0.0001

space" term (DSP), as the difference between the first dorsal insertion (D1I) less the second dorsal origin (D2O). When the analysis was run with this new variable (DSP), it was selected as an important term in the functions (Tables 4 and 9).

The centroids for yearling fish do not fall into two classes, which would have suggested either a geographic north-south or temporal spring-summer spawned classification (Fig. 1); rather they fall into three clusters of cohorts by year class, regardless of geography of collection site (Table 10). For example, collections during 1987 at Hatteras, North Carolina, and Chesapeake Bay, Virginia (the 1986 year class), are separate and distinct from both the 1988 and 1989 collections (1987 and 1988 year classes) and also from the Hatteras and Chesapeake Bay collections. Further, the 1989 collections (1988 year class) were classified into two groups, one of which was the same as the 1988 collection. The 1990 collection (1989 year class) fell in between 1988 and 1989, overlapping both.

The centroids of the large fish (>400 mm), a mixture of up to 10 year classes in a sample, showed little geographic, temporal, or year-class classification (Fig. 2).

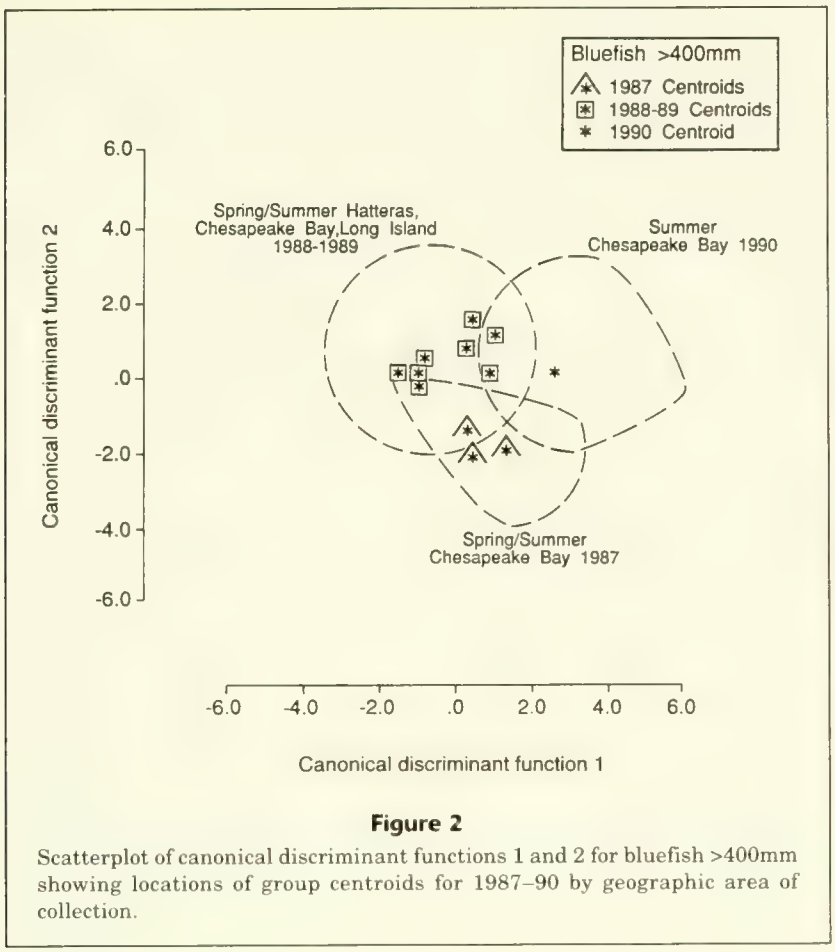

Figure 2

Scatterplot of canonical discriminant functions 1 and 2 for bluefish >400mm showing locations of group centroids for 1987–90 by geographic area of collection.

Discussion

Several authors (Nyman and Conover, 1988; McBride, 1989; Simpson et al., 1990) working in the Long Island region and analyzing length-frequency data, reported exclusively spring-spawned young-of-the-year during 1985–86. Both spring-spawned and some late arriving summer-spawned young-of-the-year were collected there in 1987, and then a shift occurred to predominantly summer-spawned fish during the summer-fall of 1988.

Because ratios continued to be similar for the yearling fish in our collections and because length frequencies were also similar, our 1987 samples from Hatteras and the Chesapeake Bay were apparently from the predominantly spring-spawned 1986 year class. Our 1988 samples, the 1987 year class, were also predominantly spring spawned but were classified morphologically separate from the 1986 year class.

Our 1989 samples (the 1988 year class) from Hatteras, Chesapeake Bay, and Long Island showed a split classification, some the same as our 1988 samples (the 1987 year class) and the rest, separate from both 1987 and 1988 year classes. The 1990 samples, from a dominant 1989 year class, collected in the Chesapeake Bay, overlapped slightly between the 1987 and 1988 year classes (Fig. 1).

If the shift from spring-spawned to summer-spawned young-of-the-year noted by the above authors for Long Island holds for Chesapeake-Hatteras yearling fish, then the morphologically distinct 1986 year class from our 1987 collections was composed of spring-spawned fish. The 1988–90 collections of the 1987–89 year classes, may be a mix of spring- and summer-spawned fish but show no separation. As stated earlier, however, our length frequencies of yearling fish in all years (1987–90) suggest that our samples were all spring-spawned fish (Table 2). An alternate explanation is that the morphologically distinct yearling fish, representing separate year classes or annual cohorts, and spawned in differing environments each year are demonstrating environmental or phenotypic plasticity. That is, that their morphological characters are environmentally determined and are different each year.

Table 8

Canonical discriminant function coefficients linear discriminant equation (Norusis, 1985): $D = B_0 + B_1X_1 + B_2X_2 + B_3X_3 \ldots\ldots B_nX_n$. See Table 3 for definitions of variables.

	Unstandardized function coefficients			
	200-400 mm FL function		>400 mm FL function	
Variable	1	2	1	2
PMX	−11.3805	−7.5218	−5.8925	−27.9831
MAX	1.2972	4.1059	8.0311	30.1133
IOB	11.3277	−0.4940	2.0227	24.8566
POB	−6.1778	−18.1707	−5.7929	−45.9063
POP	6.1848	4.7921	−5.1122	25.7729
OPC	−26.3362	6.4774	−2.5250	−29.3489
HDP	−0.6669	29.7938	26.4669	17.4505
PCO	36.7537	−2.9036	1.8195	−20.8899
PLO	10.1294	−13.7243	20.1050	−4.4471
PLI	26.8615	31.4590	−57.1219	26.6134
AFO	−31.2089	8.5720	42.9709	−2.0460
AFI	31.6723	35.3519	−24.5871	12.8353
D1O	4.0019	−3.4074	−35.3567	−8.2396
D1I	12.8394	−22.4628	48.7193	−14.1872
DSP	0.2674	3.7165	1.3185	1.3386
D2I	32.9298	−6.5686	3.9964	39.1365
CONSTANT	−212.7263	−118.6822	−45.9465	−78.7146

Table 9

Canonical discriminant function group centroid means. * = no collections from this size group

	200–400 mm		>400 mm	
Group	Function 1	Function 2	Function 1	Function 2
1	−1.1747	−2.4628	2.2954	−4.1523
2	−1.8353	−4.8299	−0.7644	−2.2536
3			−0.9446	0.5734
4	−1.4581	−2.4707	−0.4563	−2.1051
5	0.2588	1.6696	0.9954	0.6740
6	−0.4975	0.3665	1.3013	−0.0488
7		*	0.8351	−0.6780
8		*	1.4361	−0.1726
9	−1.4280	−0.0648		
10	−1.0596	0.8962		*
11	−0.7187	1.0913	−0.0650	0.3479
12	2.2186	−0.3778	−1.1776	0.1391
13			−1.5116	0.4816
14	2.7864	1.0578	−1.3068	1.6483
15	−0.2675	0.3093	−0.7993	0.5799
16	1.1706	−0.0615	−1.9122	0.4894

The larger fish in this study are a composite of at least ten year classes (2–11 years); therefore separation or classification would be expected to be less precise. Indeed there was considerable overlap in classification of the larger fish (Table 10).

From results of the DFA, and in light of the back calculations of Chiarella and Conover (1990) and the genetic data of Graves et al. (1993), it would appear that there is only one stock of bluefish in the mid-Atlantic Bight and that the morphometric differences among bluefish cohorts are a result of phenotypic plasticity. Because the environment at the time of spawning and juvenile development varies geographically and interannually, so too will morphometric features. As the fish grow, their plastic morphological characters, expressed as an index of character length versus fish length, become less and less reliable; when year classes mix, as in our >400 mm sample, they provide no discriminant characterization unless separated by individual year class.

Although a single genetic stock, the two MAB cohorts (spring- and summer-spawned), may exhibit interannual differential recruitment success and survival to yearlings. In addition, the reported differences in growth, seasons and location of spawning, migration routes, and variations in fishing mortality along the MAB can complicate management efforts if the two cohorts are managed as a single stock. Even for a single mid-Atlantic genetic stock, recruitment variations between spring and summer cohorts may be significant, year to year, and consideration should be given to monitoring the annual contribution of the spring-spawned and summer-spawned cohorts as the stock may be healthier when the spring-spawned predominate for several years running (Chiarella and Conover, 1990). The morphometric separation by year class provides evidence that the environment likely affects bluefish size and shape; this may prove to be a useful tool in separating yearling bluefish by the geographic area in which they spent their first year of development.

Conclusions

Previous larval and tagging studies neither support nor refute the existence of one or more MAB bluefish stocks, one that spawns just south of Hatteras, North Carolina, in the spring and the other off New England in the summer. The mtDNA analysis by Graves et al. (1993) suggests that there is one mid-Atlantic stock which from our results produces several environmentally induced morphotypes.

Table 10

Classification results by geographic area and year for fish 200–400 mm FL and fish >400 mm FL. SU = Summer; SP = Spring; HA = Hatteras; CB = Chesapeake Bay; LI = Long Island; PS = Pamlico Sound, NC.

Group	Group number	*n*	Predicted group membership (%)															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
200–400 mm FL																		
SU/HA/87	1	14	64	7							7			7			14	
SU/CB/87	2	10		100														
SP/CB/87	4	15	7			47					27	13					7	
SU/CB/88	5	11					46					27					9	18
SU/LI/88	6	7				29	14				29		14					14
SU/CB/88	9	104	1				1				76	14	3				3	2
SU/HA/88	10	85				1					19	61	7	1			11	
SP/HA/89	11	42									2	36	55	2			5	
SU/CB/89	12	128				1					5	2	2	79		2	3	6
SU/HA/89	14	11												64		27	9	
SP/PS/89	15	71									13	16	1	1			69	
SU/CB/90	16	26	4								4	4	15				4	69
>400 mm FL																		
SU/HA/87	1	2	100															
SU/CB/87	2	37		73		14		8						3				3
SP/HA/87	3	8			88								12					
SP/CB/87	4	30		13		70	7	7		3								
SU/CB/88	5	106				1	53	26		2			9	4		1	1	3
SU/LI/88	6	174		1			8	76	1	1			12	1	1	1		
SU/VC/88	7	13						54	39					7				
SP/CB/88	8	26		4		4	8	27	8	35			15					
SP/HA/89	11	101		2			2	5	1	3			66	7	6	5		4
SP/CB/89	12	51		2		4	4	6	2				33	35	6	6	2	
SU/LI/89	13	44		2	2	2							41	5	41	5		2
SU/HA/89	14	29					10						10		4	69		7
SU/PS/89	15	7												14			86	
SU/CB/90	16	30		7				3					11	12	7	7		47

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We wish to acknowledge the field assistance of Ana Beardsley and Jan McDowell, as well as the officials of the various Virginia bluefish tournaments that made samples available to us. Critical review was provided by John Graves and Jack Musick of VIMS. The most helpful comments of an anonymous reviewer strengthened the manuscript and we are most grateful to this anonymous colleague. The work was supported by a grant to the Virginia Institute of Marine Science from the U. S. Fish and Wildlife Service, through the Virginia Marine Resources Commission, grant n number F-60-R.

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Estimates of exploitation rates for north Pacific albacore, *Thunnus alalunga*, from tagging data

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Abstract.—North Pacific albacore tagging data from a tag-release program conducted from 1971 to 1989 were analyzed to obtain estimates of exploitation rates and related parameters. The major albacore fishing fleets in the North Pacific, the U.S. baitboat, Japan baitboat, troll and longline fleets were used in the analysis. Another category of fleet ("other") that combined remaining miscellaneous recapture sources was also used. Tag-attrition models incorporating variable availability of tagged albacore to the various fleets, seasonal catchability, and multiyear effects on catchability were developed and applied. The incorporation of all three effects was found to improve model fit significantly. If exploitation of the tagged population is representative of the North Pacific albacore population as a whole and if tag reporting rates were high, the results would suggest that the exploitation rate has been less than 10% per year since the early 1970s. However, a deficit of returns from the troll fleet in comparison with its catch suggested that the pattern of exploitation of the tagged population, by this fleet at least, was different from that for the untagged albacore population. After compensating for assumed depressed availability of tagged albacore to the troll fleet, annual exploitation rates were estimated to have declined from a high of 40% in the mid-1970s to <10% since the early 1980s.

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Albacore tuna, *Thunnus alalunga*, occur in the tropical and subtropical waters of the Pacific Ocean, where they comprise separate stocks north and south of the equator (Murray, 1994). In the north Pacific, albacore spawn predominantly in the spring and summer over a wide area bounded approximately by 10°–30°N (Nishikawa et al., 1985). Juvenile albacore appear in the North Pacific Transition Zone (35°–45°N), where they are exploited by the surface fishery, comprising mainly Japanese and U.S. baitboat, troll, and until the early 1990s, Japanese and Taiwanese driftnet fleets (Fig. 1). Adult albacore are found at lower latitudes, where they are caught by the subsurface longline fishery, comprising Japanese, Korean, and Taiwanese fleets (Fig. 1). Longline catches have been fairly stable at 10,000–20,000 t annually. Total surface fishery catches (which have been dominated by Japanese baitboat catches) have declined from a peak of around 100,000 t in the mid-1970s to 20,000–50,000 t in recent years (Liu and Bartoo, 1995).

Since 1971, 23,780 albacore have been tagged in the North Pacific in a program conducted jointly by the U.S. National Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation. The tag recoveries have been used in studies of albacore movements (Laurs and Lynn, 1977), growth (Laurs and Wetherall, 1981), and fishery interaction (Kleiber and Baker, 1987). However, to date no formal analysis of the data has been undertaken to estimate exploitation rates and related parameters. In this paper, we develop tag-attrition models (Kleiber et al., 1987), incorporating different structural assumptions concerning availability and catchability of the tagged population. The models are fitted to the albacore tagging data to obtain estimates of the instantaneous rate of natural mortality and fleet-specific catchability coefficients. These estimates are used to construct time series of estimated exploitation rates. The relative merits of the alternative models and applicability of the estimates to the North Pacific albacore population in general are discussed.

Materials and methods

Tagging data

Albacore tagging occurred from 1971 to 1996, mainly during April–Sep-

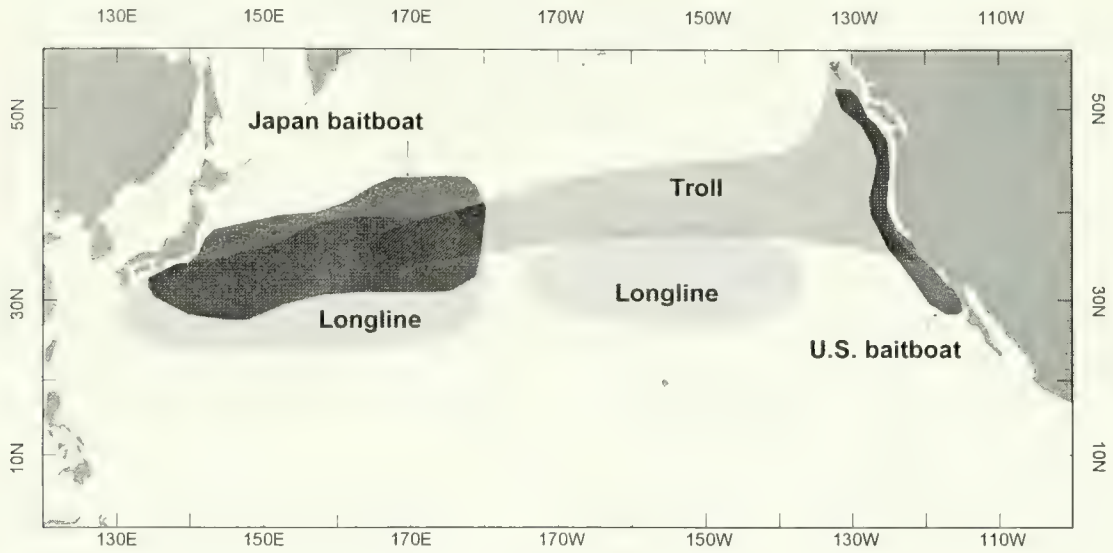

Figure 1
Schematic diagram of geographic distributions of major North Pacific albacore fishing fleets.

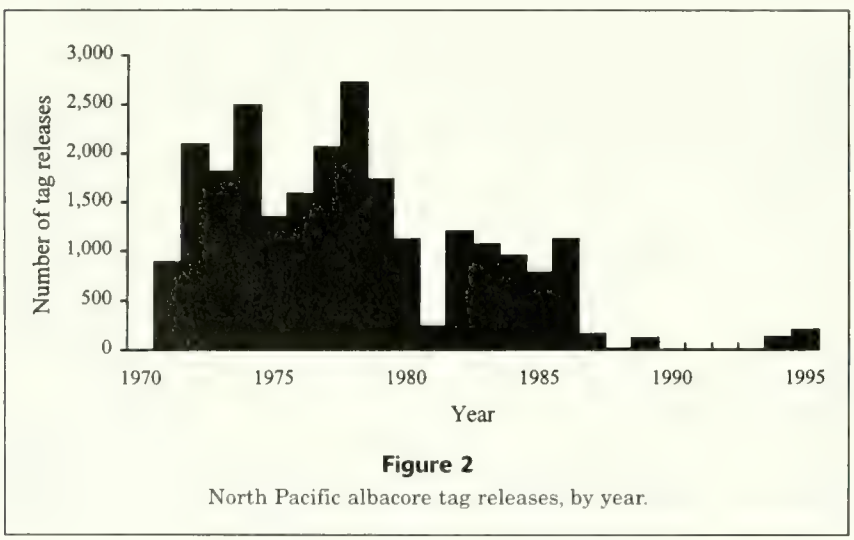

Figure 2
North Pacific albacore tag releases, by year.

tember, with 97% of the 23,780 releases occurring prior to 1987 (Fig. 2). Tagging was carried out aboard U.S. troll vessels and baitboats by NMFS technicians and commercial fishermen trained in tagging. Tagging methods are described by Laurs et al. (1976) and Laurs and Wetherall (1981). Only albacore judged to be in very good condition were selected for tagging; therefore mortality due to tagging is believed to have been negligible. Tagged albacore were released over a wide area of the eastern and central North Pacific; the largest numbers of releases took place in coastal waters adjacent to North America at 30°–50°N (Fig. 3). Fewer albacore were tagged west of 180°, which is the main operational area of the Japanese baitboat fleet. The size distribution of tagged albacore is typical of surface fishery catches (Fig. 4).

As of 14 August 1997, 1302 tagged albacore (5.5% of the releases) had been recaptured and the tags returned to NMFS. Recaptures have been recorded from a wide range of national fleets and gear types, but the largest numbers of recaptures (68% of the total) were made by U.S. and Japanese baitboats and U.S. troll boats (Table 1). Recaptures occurred throughout the North Pacific, but most recaptures were concentrated in coastal waters adjacent to North America (mainly U.S. troll and baitboats) and west of 180° (Japanese baitboats) (Fig. 5).

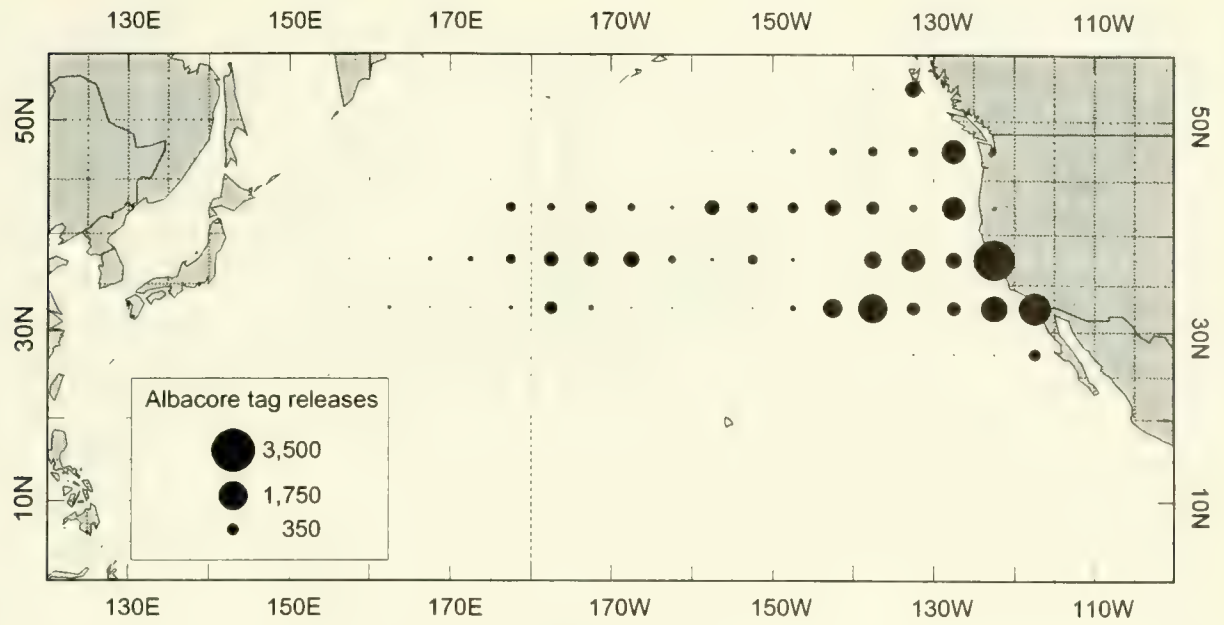

Figure 3
Geographical distribution of North Pacific albacore releases, 1971–89

Population dynamics model for tagged albacore

We used a tag-attrition model (e.g., Seber, 1973; Kleiber et al., 1987) to describe the dynamics of tagged albacore (hereafter referred to simply as "tags"). The model may be represented by

$$\hat{r}_{ijf} = R_i(1-\alpha)\beta\gamma \exp\left[-\sum_{k=1}^{j-1}\sum_f (F_{ikf}) - (j-1)(M+\psi)\right] \frac{F_{ijf}}{\sum_f F_{ijf} + M + \psi}\left[1-\exp\left(-\sum_f F_{ijf} - M - \psi\right)\right], \quad (1)$$

where $\hat{r}_{ijf}$ = the estimated number of tags from release group i recaptured by fleet f in time period j and returned with complete information (recapture time and fleet);
R_i = the number of tags released in release group i;
α = the proportion of type-1 tag losses;
β = the proportion of recaptured tags that are returned;
γ = the proportion of returned tags having complete information;
F_{ijf} = the instantaneous rate of fishing mortality on release group i in time period j by fleet f;
M = the instantaneous rate of natural mortality;
ψ = the instantaneous rate of type-2 tag loss;
i = an index for release group;
j = an index for time period;
k = an index for time periods prior to j; and
f = an index for fleet.

Data stratification

In order to allow seasonal variability in tag returns to be modeled, tag releases and returns were grouped by the quarter (Jan–Mar, Apr–Jun, Jul–Sep, and Oct–Dec) and year of release and recapture. This resulted in 48 release groups (Table 2). Small numbers of releases in 1994 and 1995, from which no recaptures have so far been reported, were not included in the analysis. We defined five fleets: 1) U.S. baitboat; 2) Japanese baitboat; 3) U.S. and Canadian troll (referred to as the troll fleet); 4) Japanese, Korean, and Taiwanese longline (referred to as the longline fleet); and 5) others (consisting of recapture sources not otherwise defined). This definition was designed to group fleets having similar characteristics (fishing methods, seasonal distributions of effort, and sizes of albacore caught). The observed tag returns, r_{ijf}, were thus grouped by tag release group (i), quarter and year of recapture (j), and recapture fleet (f). Tag returns to the end of 1992 were considered in the analysis.

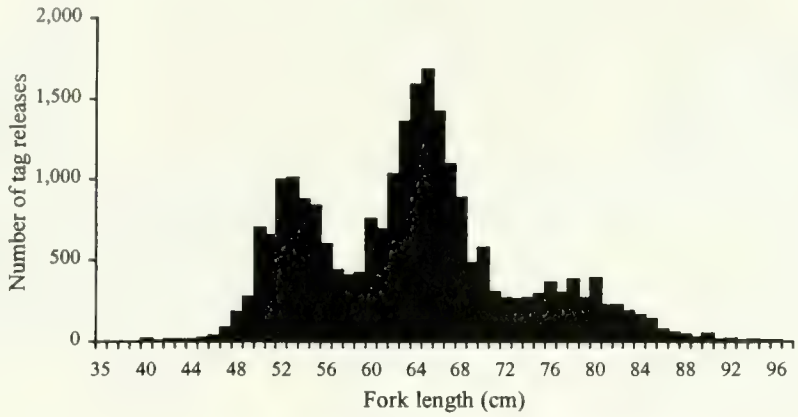

Figure 4
Size distribution of North Pacific albacore tag releases, 1971–89.

Table 1
Number of albacore tag returns in the North Pacific, 1971–1992, by recapture fleet.

Vessel or gear type	Nationality	Number of returns	%
Baitboat		715	56.3
	U.S.	403	
	Japan	312	
Troll		148	11.7
	U.S.	146	
	Canada	2	
Sport		137	10.8
	U.S.	135	
	Japan	2	
Longline		79	6.2
	Japan	61	
	Korea	15	
	Taiwan	2	
	Unknown	1	
Purse seine		39	3.1
	U.S.	34	
	Japan	4	
	Mexico	1	
Drift gill net		29	2.3
	U.S.	1	
	Japan	24	
	Canada	1	
	Taiwan	3	
Handline		5	0.4
	U.S.	5	
Unknown		117	9.2
	U.S.	112	
	Japan	2	
Unknown		3	
Total		1269	100.0

Nuisance parameters

We assumed that tag shedding was the only source of type-1 and type-2 tag loss and therefore used values for α and ψ of 0.12 and 0.0245 per quarter, respectively, based on analysis of double-tagging data (Laurs et al., 1976). There are no independent estimates of nonreporting of North Pacific albacore tags, although Kleiber and Baker (1987) stated that "nonreporting losses are small for the major fisheries that recovered the tags"; they assumed $\beta = 0.9$. We also made this assumption but tested the sensitivity of our results to values of β in the range 0.1 to 1.0. The value of γ(0.87) was estimated directly from the tag-return data.

Reparameterization of fishing mortality

To create sufficient degrees of freedom to enable a statistical estimation of parameters, the number of fishing mortality parameters to be estimated, F_{ijf} needs to be reduced. If we assume for the moment that F_{ijf} is independent of release group i, F_{jf} may be reparameterized as a function of fishing effort, E_{jf}, and catchability, q_{jf}:

$$F_{jf} = q_{jf} E_{jf}. \quad (2)$$

We may then propose models that constrain q_{jf} in some sensible way. Let S_{jf} denote a matrix that contains, for each f, a season for each time period indexed by j. We tested two seasonal schemes: no seasonal variation for any fleet and seasonal variation (Q1=Jan–Mar, Q2=Apr–Jun, Q3=Jul–Sep, Q4=Oct–Dec) for all fleets.

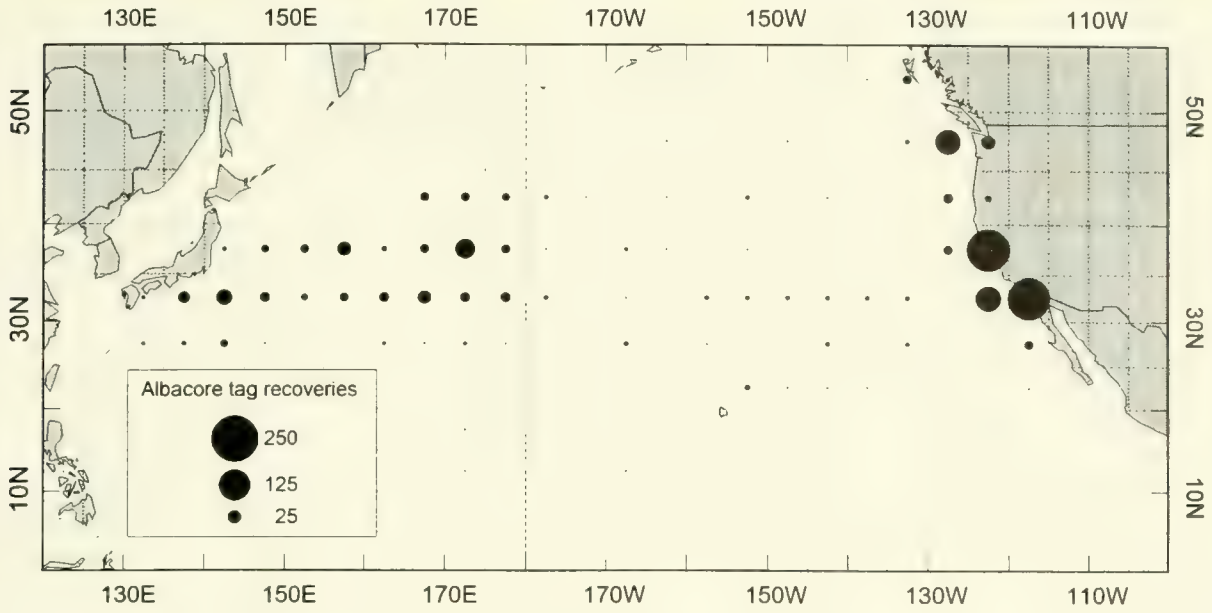

Figure 5
Geographical distribution of North Pacific albacore recoveries, 1971–92

Additionally, we tested constraints on q_{jf} that specified how catchability might vary over longer (multiyear) time periods. Let T_{jf} be a matrix that, for each f, maps time period j into a series of multiyear periods within which the seasonal pattern of catchability for that fleet may be assumed to be constant. We tested two schemes for T_{jf}: a constant pattern of catchability over time for all fleets and catchability patterns for all fleets specific to four time periods (1=1971 Q4 to 1974 Q4, 2=1975 Q1 to 1979 Q4, 3=1980 Q1 to 1984 Q4, and 4=1985 Q1 to 1992 Q4). Incorporating the notation for seasonal and multiyear effects, Equation 2 may then be rewritten as

$$F_{ij} = q_{S_i T_j} E_{ij}. \quad (3)$$

Quarterly effort statistics for fleets 1 and 3 were obtained from NMFS databases. Statistics for fleets 2 and 4 were obtained from Secretariat of the Pacific Community databases. An arbitrary, constant level of effort was assumed for fleet 5. Effort data were compiled for the period from 1971 Q4 to 1992 Q4 to correspond to the period of the tagging experiment.

Changes in availability of the tagged population

The model as described thus far implies that the availability of the tagged population to the various fisheries remains constant for the duration of the experiment. There are two reasons why this assumption may not be satisfied, necessitating some adjustment to the model. First, the spatial distribution of the tagged population of any release set in relation to the spatial distribution of fishing effort by the recapture fleets was not constant over time. In particular, because most releases occurred in the eastern Pacific, the tagged population would have been initially more available to the U.S. baitboat and troll fleets and less available to the Japanese baitboat and longline fleets, which have a more westerly distribution. Over time, as the tagged population dispersed, the effects of such differential spatial availability would be expected to dissipate. Second, the availability of the tagged population to the recapture fleets would also be affected by the size distribution of the tagged population. Tagged fish at release were generally of a size similar to sizes of fish captured by the surface fisheries but were considerably smaller than those captured by the longline fishery. Therefore, the availability of the tagged population at release would not be limited initially by size for the surface fisheries but would be reduced for the longline fishery. As the tagged fish grew, their availability to the longline fishery would become less restricted by their size, but their availability to the surface fisheries might be reduced as they "grew out" of the size range typically exploited by those fisheries. Because our model has neither spatial nor size structure, the effects of size and spatial distributions cannot be explicitly incorporated. However, we developed an approximate means to allow for such effects in ag-

Table 2
North Pacific albacore tag-release and tag-return data, summarized by release group.

	Releases		Returns						
			With recapture date						
Group	Date (qtr/yr)	Number	U.S. baitboat	Japan baitboat	Troll	Longline	Other	Recapture date unavailable	Total
1	4/71	887	13	6	1	0	7	6	33
2	2/72	1110	42	10	2	3	11	15	83
3	3/72	976	48	3	4	2	27	14	98
4	2/73	1611	50	19	10	2	4	22	107
5	3/73	182	1	2	0	0	1	1	5
6	4/73	12	0	0	0	0	0	0	0
7	2/74	1379	39	23	5	2	3	12	84
8	3/74	1006	31	36	2	4	2	8	83
9	4/74	101	1	2	1	0	3	1	8
10	2/75	406	1	6	0	0	5	1	13
11	3/75	902	39	10	9	2	23	16	99
12	4/75	41	2	0	1	0	1	1	5
13	2/76	449	7	1	1	0	5	3	17
14	3/76	1115	32	7	6	3	11	14	73
15	4/76	17	0	0	0	0	1	0	1
16	1/77	1	0	0	0	0	0	0	0
17	2/77	63	1	2	0	1	0	1	5
18	3/77	1725	22	18	20	5	35	13	113
19	4/77	273	3	0	2	3	3	2	13
20	2/78	236	0	11	1	3	2	1	18
21	3/78	2196	21	29	56	15	27	16	164
22	4/78	290	2	1	1	2	3	1	10
23	2/79	272	0	8	0	2	0	1	11
24	3/79	1451	8	21	11	7	9	8	64
25	2/80	199	0	0	0	0	0	1	1
26	3/80	897	1	18	0	1	8	4	32
27	4/80	19	0	0	0	0	1	0	1
28	1/81	56	0	0	1	0	0	0	1
29	3/81	189	0	1	1	1	3	1	7
30	1/82	13	0	0	1	0	0	0	1
31	2/82	173	0	1	0	0	2	0	3
32	3/82	991	0	22	0	2	7	1	32
33	4/82	23	0	0	0	0	0	0	0
34	2/83	463	0	9	0	5	3	0	17
35	3/83	584	1	15	2	1	3	1	23
36	4/83	14	0	0	0	0	0	0	0
37	2/84	558	0	8	0	2	1	0	11
38	3/84	382	0	4	0	2	3	1	10
39	4/84	8	0	0	0	0	0	0	0
40	2/85	452	0	3	0	0	3	0	6
41	3/85	331	0	1	0	0	1	0	2
42	4/85	2	0	0	0	0	0	0	0
43	2/86	502	0	3	0	1	1	1	6
44	3/86	619	0	1	0	0	3	3	7
45	2/87	63	0	0	0	0	0	0	0
46	3/87	94	0	0	0	0	0	0	0
47	3/88	6	0	0	0	0	0	0	0
48	3/89	110	0	0	0	1	0	1	2
Total		23,449	365	301	138	72	222	171	1269

gregate in order to reduce the potential bias in the other parameter estimates of interest. We defined a fleet-specific availability coefficient, $\phi_{t_{ij}f}$, where the index t_{ij} refers to the number of time periods at liberty of release group i in time period j. Equation (3) then becomes

$$F_{ijf} = \phi_{t_{ij}f} q_{S_i T_j} E_{jf} \quad (4)$$

$\phi_{t_{ij}f}$ is therefore a proxy variable related to time at liberty that we used to correct, in an approximate way, for the effects of changing availability of the tagged population over time. However, $\phi_{t_{ij}f}$ need not be estimated for all t_{ij}. Rather, ranges of t_{ij} may be specified for which the $\phi_{t_{ij}f}$ are considered to be constant at either 0 (completely unavailable) or 1 (fully available).

A scheme for constraining $\phi_{t_{ij}f}$ was devised from preliminary inspection of the data, and some knowledge of albacore dispersion (Laurs and Lynn, 1977), growth (Laurs and Wetherall, 1981), and gear selectivity (Bartoo and Holts, 1993) in the North Pacific (Table 3). The scheme provided three time periods for spatial mixing of tagged albacore with respect to the surface fishery fleets and the "other" fleet (which has characteristics similar to the surface fishery fleets), and eight time periods to allow recruitment of tagged albacore to the longline fishery. During these periods, $\phi_{t_{ij}f}$ was estimated from the data. We assumed that tagged albacore remain fully available to the longline fishery during the constrained period for ($\phi_{t_{ij}f}$ =1 for t_{ij}>8). For the surface fishery and "other" fleets, this may not be a good assumption, because these fishing methods may not have fully selected albacore of larger size (Bartoo and Holts, 1993). Therefore, we assumed that albacore were fully available during periods 4–11 after release ($\phi_{t_{ij}f}$ =1 for 3<t_{ij}<12) but were completely unavailable to these fleets after 15 time periods ($\phi_{t_{ij}f}$ =0 for t_{ij}>15).

Table 3

Scheme used to define variation in tagged albacore population availability. See text for definition of symbols.

	t_{ij} (quarters)			
Fleet	$\phi_{t_{ij}f}$ estimated	$\phi_{t_{ij}f}$ = 1	$\phi_{t_{ij}f}$ estimated	$\phi_{t_{ij}f}$ = 0
U.S. baitboat	1–3	4–11	12–15	>15
Japanese baitboat	1–3	4–11	12–15	>15
Troll	1–3	4–11	12–15	>15
Longline	1–8	>8	—	—
Other	1–3	4–11	12–15	>15

To allow for a gradual decline in availability during the intermediate period (11<t_{ij}<16), $\phi_{t_{ij}f}$ was estimated from the data.

Parameter estimation

We used a multinomial likelihood function to fit the various models to the tagging data. A derivation of the likelihood function as applied to tagging data is given in Kleiber and Hampton (1994). We minimized the negative log of this function to obtain the parameter estimates, i.e. by minimizing (omitting terms dependent only on the data)

$$-\sum_t \left[\left(R_t - \sum_k r_{tk}\right) \ln\left(1 - \frac{\sum_k \hat{r}_{tk}}{R_t}\right) + \sum_k r_{tk} \ln\left(\frac{\hat{r}_{tk}}{R_t}\right) \right], \quad (5)$$

where the k subscript indicates an individual recapture stratum (combining recapture period, fleet, and time at liberty dimensions). Minimization was carried out with a quasi-Newton routine (Otter Research, 1991). The variance-covariance matrix of the estimated parameters was estimated from the inverse of the Hessian matrix (Bard, 1974). The variance of quantities that are functions of the estimated parameters (such as exploitation rates) were determined by the delta method (Seber, 1973).

Results

Model fits

Eight different model formulations, based on different combinations of constant or variable availability, constant or seasonal catchability, and presence or absence of multiyear effects on catchability, were fitted to the North Pacific albacore tagging data. The total numbers of estimated parameters and the maximum log-likelihood function values for each fit are shown in Table 4. It is clear that the addition of variable availability, seasonal catchability, and multiyear effects on catchability all result in highly significant improvements in fit. The model incorporating all three effects, model 8, is suggested as the most appropriate of the tested models on the basis of likelihood-ratio tests (Kendall and Stuart, 1979). Model 6, which did not incorporate multiyear catchability effects, was the next preferred model.

Examples of plots of observed and predicted tag returns, aggregated over tag release groups, are shown in Figure 6 for model 2 and in Figure 7 for model 8. As expected, there are large discrepancies

Table 4

Maximum log-likelihood function values for alternative model formulations comprising constant (–) or variable (+) availability, constant (–) or seasonal (+) catchability, and absence (–) or presence (+) of multi-year effects on catchability.

Model number	Variable availability	Seasonal catchability	Multi-year effects on catchability	Number of parameters	Log likelihood
1	–	–	–	6	–9,511.2
2	–	+	–	19	–9,210.7
3	–	–	+	19	–9,386.1
4	–	+	+	50	–9,036.9
5	+	–	–	37	–9,089.9
6	+	+	–	47	–8,834.4
7	+	–	+	47	–8,973.3
8	+	+	+	79	–8,666.5

Table 5

Estimates of natural mortality rate M and $\phi_{t,f}$ obtained from fitting model 8 (see Table 4) to the North Pacific albacore tagging data. Underlined zeros indicate parameters set to zero because of zero tag return in those time periods.

	Recapture fleet											
	U.S. baitboat		Japan baitboat		Troll		Japan longline		Other			
Parameter	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV	Estimate	CV
M (1 year)	0.608	0.090										
ϕ_{1f}			0.176	0.207	0.035	0.510	0.408	0.252	0.000	—	0.774	0.174
ϕ_{2f}			0.256	0.168	0.067	0.601	0.802	0.231	0.000	—	0.344	0.269
ϕ_{3f}			0.297	0.273	0.169	0.511	0.286	0.755	0.056	0.626	0.900	0.424
ϕ_{4f}									0.103	0.763		
ϕ_{5f}									0.000	—		
ϕ_{6f}									0.414	0.470		
ϕ_{7f}									0.306	0.406		
ϕ_{8f}									0.212	0.741		
ϕ_{12f}			0.277	1.012	0.299	0.398	1.000	—			0.654	0.731
ϕ_{13f}			0.415	0.594	0.554	0.469	0.313	1.015			0.290	0.723
ϕ_{14f}			0.486	0.470	0.237	1.018	0.000	—			0.679	0.600
ϕ_{15f}			0.000	—	0.260	1.016	0.000	—			0.000	—

between observed and predicted returns for model 2, particularly in the time periods soon after release. Major discrepancies were eradicated in the model 8 fit, which has greater flexibility in fitting the returns for these initial periods. Notice also that model 8 not only better predicts the returns for time periods in which $\phi_{t,f}$ was estimated (periods 1–8 for the longline fleet, periods 1–3 and 12–15 for all other fleets) but performs much better in predicting returns from periods of assumed full availability as well (e.g. periods 5 and 6 for U.S. baitboat and troll, periods 10–15 for longline).

Parameter estimates

Estimates of M and $\phi_{t,f}$ for the model 8 fit (β=0.9) are given in Table 5 by way of example. The model 8 estimate of M (0.608/yr, coefficient of variation 0.09) is similar to estimates obtained by Bertignac et al.[1] from albacore tagging data in the South Pacific but

[1] Bertignac M., P. Lehodey, and J. Hampton. 1996. An analysis of the South Pacific albacore tagging data: estimation of movement patterns, growth and mortality rates. 6th South Pacific Albacore Research Group meeting; 5–7 March 1996. [Available from senior author.]

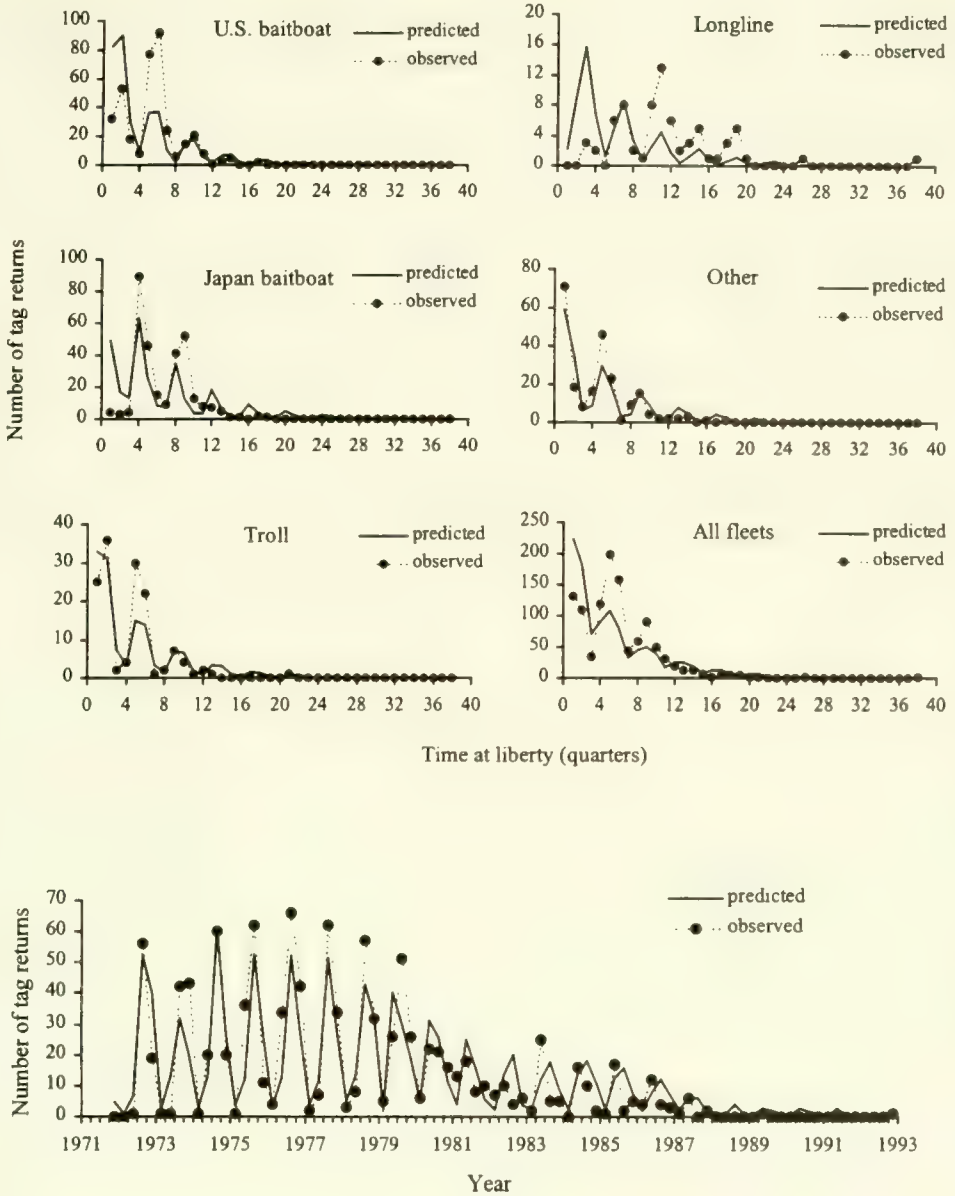

Figure 6

Observed tag return numbers and tag returns predicted with model 2 (see Table 4 for description).

higher than previous estimates obtained from fishery data by Suda (1966) and Fournier et al. (1998). Model 1–4 estimates of M (0.496–0.536/yr) are lower than those of models 5–8 (0.576–0.632/yr) because in the former, the models attempt to accommodate the low numbers of initial tag returns by depressing M, whereas in the latter, reduced availability for the initial time periods rather than reduced M is found to be a more likely solution. We noted that the correlation coefficients between the estimates of M and the $\phi_{t_{i,f}}$'s for the initial time periods were always negative and were in the range of –0.09 to –0.45.

The coefficients of variation of the $\phi_{t_{i,f}}$ estimates were variable (0.16–1.0) and were particularly high for the surface fleets at time periods at liberty beyond three years when very few tagged albacore were recovered.

For model 8, considerable differences in catchability estimates among time periods for all fleets were detected, although no consistent trends were evident (Fig. 8). The confidence intervals on these estimates were large in some cases.

Estimates of the total exploitation rate (percentage of the population harvested) in year y, calculated by

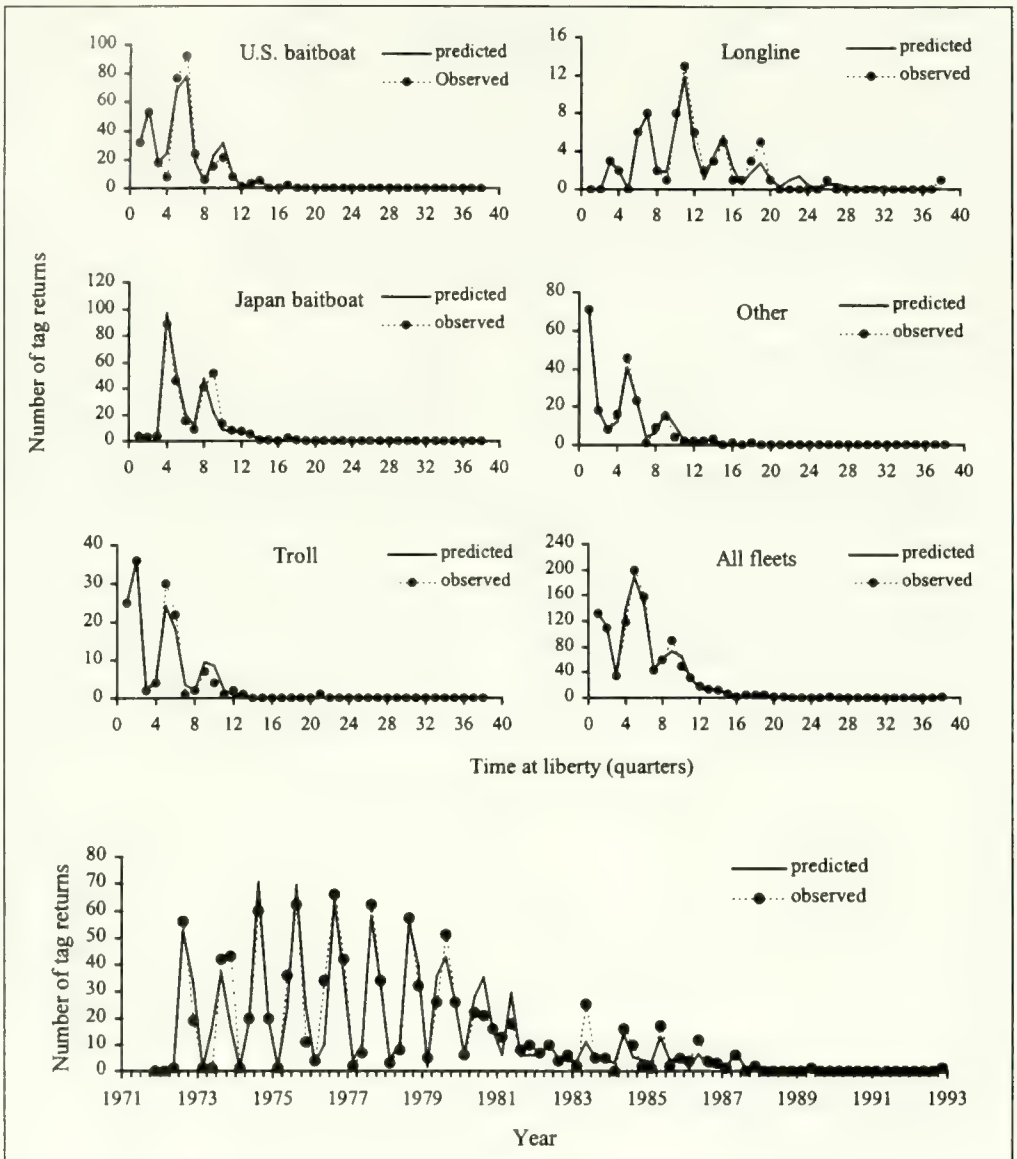

Figure 7

Observed tag return numbers and tag returns predicted with model 8 (see Table 4 for description).

$$\frac{\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf}}{\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf} + M} \tag{6}$$

$$\left[1 - \exp\left(-\sum_f \sum_k q_{S_{kf} T_{kf}} E_{kf} - M\right)\right] \times 100\%,$$

where k is a quarter occurring in year y, are shown in Figure 9 (model 8, β=0.9). Estimated exploitation rate has been <10% for most of the time series; it declined between 1976 and 1988 and increased slightly afterwards.

Effect of assumed tag reporting rate

Although the tag-reporting rate is thought to have been high for North Pacific albacore (Kleiber and Baker, 1987), this contention is not supported by independent data. We therefore examined the sensitivity of the results to different values of β (assumed to apply equally to each fleet) for the model 8 fit. The estimates of M were directly related to β; conversely, average exploitation rate was inversely related to β (Fig. 10). In both cases, the sensitivity was slight for $\beta > 0.6$. If the tag-reporting rate was above this level for the main fleets, the results of our analysis should have been robust to small departures from the assumed value.

In the absence of other information, the tag-reporting rate was assumed to be constant over time. It is possible that reporting could have varied over time, owing to variation in the effectiveness of tag recovery procedures or cooperation of fishing fleets. Although it is not possible to test conclusively such hypotheses with the available data, we might note that the time-related variability in catchability estimated with model 8 (Fig. 8) could equally have been interpreted as variation in reporting rates, because catchability and reporting rate are highly correlated in these models.

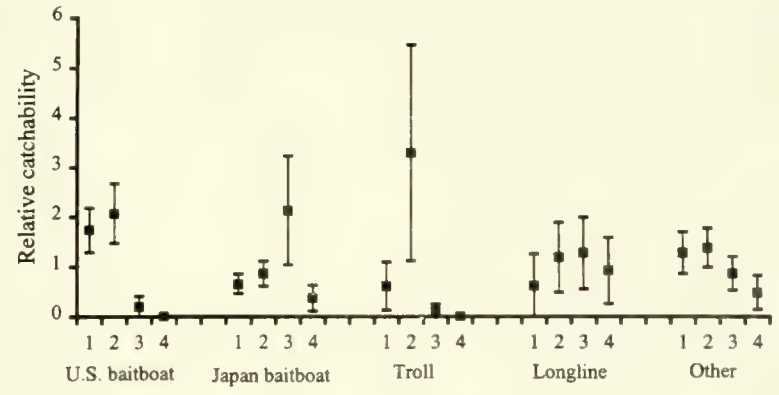

Figure 8

Estimated relative catchability (seasonally averaged and normalized within fleet categories) by multiyear time period, with 95% confidence intervals. 1=1971 Q4 to 1974 Q4, 2=1975 Q1 to 1979 Q4, 3=1980 Q1 to 1984 Q4, 4=1985 Q1 to 1992 Q4.

Discussion

The use of a tagged sample of the population to infer characteristics of the population in general is a common technique in fisheries stock assessment. For such inferences to be valid, several assumptions, discussed in detail by Seber (1973), need to hold. For North Pacific albacore, the assumption of equal probabilities of capture of tagged and untagged fish is likely to be critical. As noted earlier, both the spatial distribution of the tagged population in relation to recapture effort, and the size distribution of the tagged fish in relation to the size-selective characteristics of the different fishing gears are likely to result in violation of this assumption. We have developed a procedure to correct for these deficiencies in an approximate way. The procedure uses time-at-liberty information and knowledge of appropriate time lags to provide some correction for nonuniform availability of the tagged population to the various fishing fleets that is due to spatial and size effects. A more elegant approach would be to develop a model that explicitly deals with the spatial and size structure of the tagged population and with the spatial distribution and size selectivity of fishing effort. Spatially disaggregated tag models are now available (e.g. Kleiber and Hampton, 1994; Sibert et al., in press). An extension of such a model to include size or age structure would provide an improved method for analyzing the North Pacific albacore data.

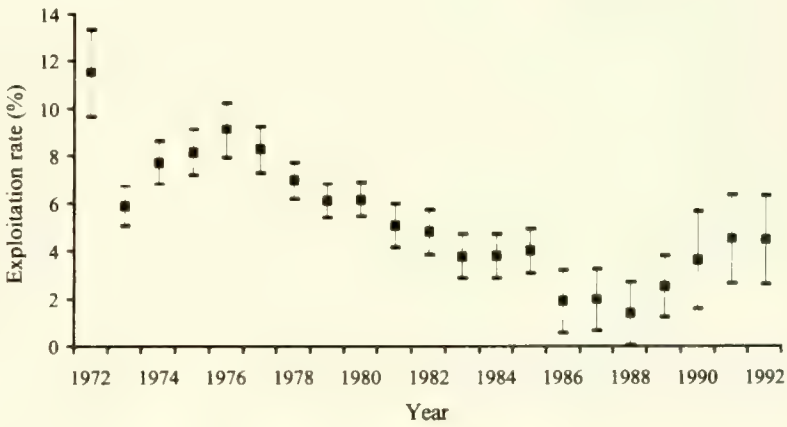

Figure 9

Time series and 95% confidence intervals of estimated annual exploitation rates of North Pacific albacore obtained for model 8 (see Table 4 for description).

The natural mortality rate parameter estimated from tagging data in this study is higher than some previous estimates for albacore. We have shown that M will be overestimated if the tag-reporting rate is overestimated. Although tag reporting for the major fleets is believed to have been high, it is possible that unreported tag recaptures by the drift gillnet fleet, which reported relatively few recaptures, have resulted in a positive bias in our estimate of M.

If the exploitation of tagged albacore is similar to exploitation of the North Pacific population in general, our results suggest that aggregate exploitation rates declined from the mid-1970s to 1988, after which some increase occurred. The results of our preferred model (model 8) further suggest that an-

nual total exploitation rates have been less than 10% during most of the years of the experiment. However, there is a strong indication that exploitation of tagged albacore by the troll fleet may not be representative of exploitation patterns generally by this fleet. The total number of tag returns from the troll fleet was 148 (Table 1). The U.S. baitboat fleet, which fished in an area similar to that fished by the troll fleet during the 1970s and 1980s, reported 403 tag recaptures. However, during the period of the tagging experiment, troll catches were some eight times baitboat catches (Liu and Bartoo, 1995). There is no ready explanation for this inconsistency. One possibility is that differential reporting rates existed between the fleets. However, given the earlier assertion that tag-reporting rates were high in general, differential tag reporting is unlikely to be the cause of such a discrepancy. Another possibility is that albacore become "hook shy" after they have been captured by trolling and are thereafter less likely to respond to trolled lures. Because the majority of albacore tag releases were troll-caught, such behavior would render the tagged population less available to the troll fleet than the albacore population in general. If this was indeed the reason for the paucity of troll-caught returns, relative availability of tagged albacore to the troll fleet would need to be of the order of 3.5% (compared with 100% for the U.S. baitboat fleet) to reconcile the tag-return and catch data for these fleets. Such reduced availability would result in significant underestimation of exploitation rates if not explicitly accounted for in the analysis. If we set $\phi_{tf} = 0.035$ for $3<t<16$ for the troll fleet, estimated exploitation rates that would apply to the untagged population are considerably higher, declining from around 40% in the 1970s to less than 10% since the mid-1970s (Fig. 11). At this point, we cannot be sure that the "hook shy" hypothesis is viable or not; therefore, both of the time series shown in Figure 11 should be considered as equally valid possibilities until additional information becomes available.

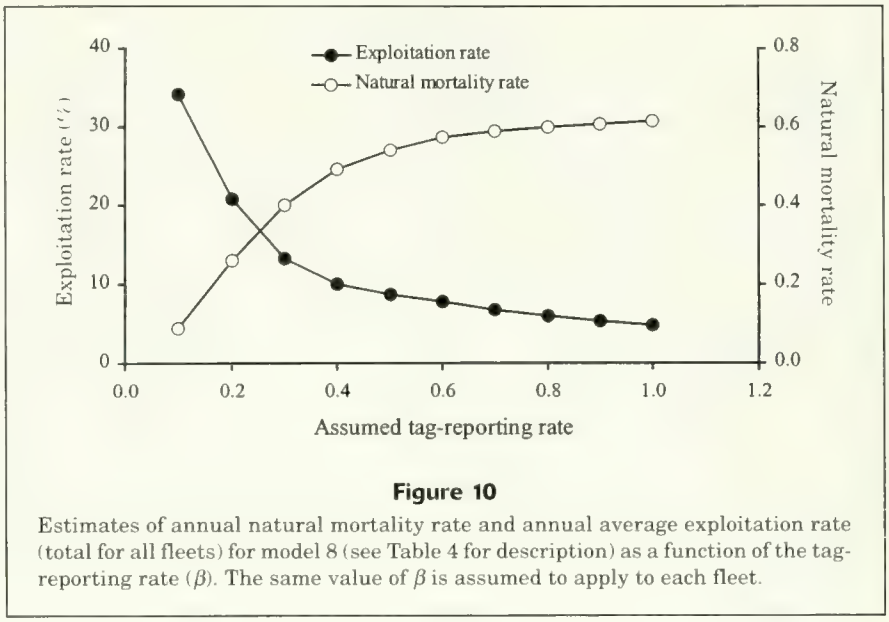

Figure 10

Estimates of annual natural mortality rate and annual average exploitation rate (total for all fleets) for model 8 (see Table 4 for description) as a function of the tag-reporting rate (β). The same value of β is assumed to apply to each fleet.

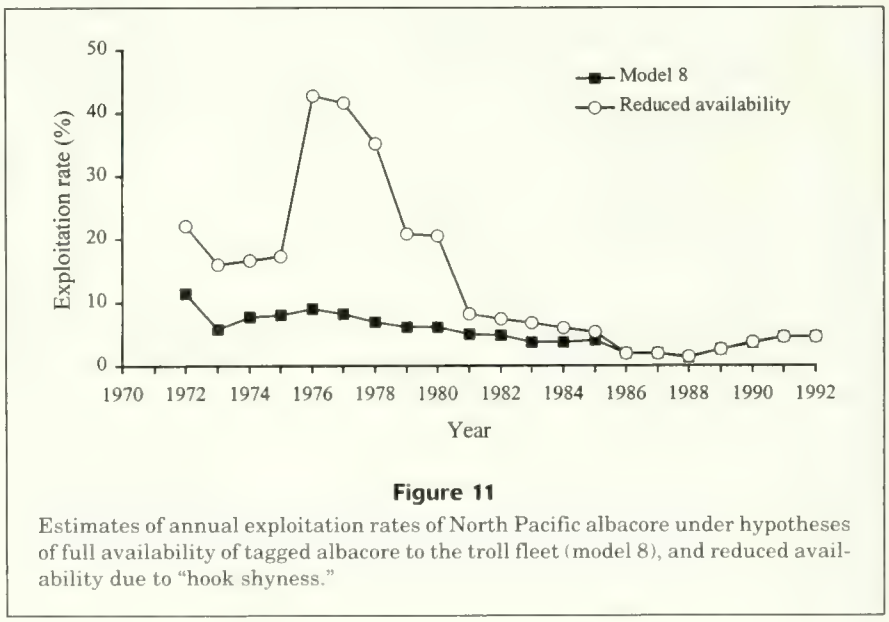

Figure 11

Estimates of annual exploitation rates of North Pacific albacore under hypotheses of full availability of tagged albacore to the troll fleet (model 8), and reduced availability due to "hook shyness."

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Use and success of composite square-mesh codends in reducing bycatch and in improving size-selectivity of prawns in Gulf St. Vincent, South Australia

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Abstract.—In response to recent voluntary adoption of square-mesh codends by commercial prawn trawlers in Gulf St. Vincent, Australia, two new designs of composite square-mesh codends were investigated for their utility in 1) reducing the bycatch of fish and 2) improving size-selectivity of the targeted prawns. The two designs (termed the composite-square-2 and the composite-square-3 codends) comprised mainly large sections of 52-mm netting hung on the bar but had different hanging ratios, tapers, and small diamond-mesh sections. A strategically located panel of 85-mm netting was inserted on the bar into the tops of the anterior sections of each codend to allow small fish to escape. Simultaneous comparisons with a conventional diamond-mesh codend (control) showed that both square-mesh designs significantly reduced the incidental capture of commercially important fish (by up to 96.9%). The numbers of prawns (*Penaeus latisulcatus*) were significantly reduced in both composite square-mesh codends (by up to 12.1%) but there was no significant reduction in weights of prawns. There were no significant differences in the selectivity parameters for prawns between the two designs. The results are discussed in terms of the probable effects that the different square-mesh configurations had on escape of fish and size-selectivity of prawns.

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Traditionally configured prawn trawls contain small diamond-shaped meshes in the codend and are not particularly selective fishing gears. In addition to the targeted prawns, they often retain large quantities of nontarget organisms, collectively termed bycatch (for reviews see Andrew and Pepperell, 1992; Alverson et al., 1994). In many prawn-trawl fisheries, this bycatch consists of a diverse assemblage of small fish, cephalopods, and crustaceans, including prawns smaller than optimal commercial size. The mortality of large quantities of juveniles of commercially or recreationally important species, or both, is of major concern, because it may deleteriously affect the recruitment and biomass of stocks targeted by other fisheries. Regulating selectivity of trawls to the desired size of prawns at first capture will also help to optimize yield and maintain sustainability of prawn stocks.

During the past decade, many studies have attempted to improve selectivity of prawn-trawl fisheries by altering the codends of trawls. Most of these studies can be categorized into examinations of 1) bycatch reducing devices (BRDs) that facilitate the escape of unwanted fish (e.g. Watson et al., 1986; Broadhurst and Kennelly, 1997; Rogers et al., 1997); or 2) different sizes, shapes, and configurations of mesh that improve selectivity of the targeted species by reducing the bycatch of conspecifics (e.g. Karlsen

and Larsen, 1989; Tokai et al., 1990; Thorsteinsson, 1992; Tokai and Sakaji, 1993). However, to minimize biological impacts on bycatch and to promote ecologically sustainable fisheries, prawn trawls should be modified to address both these issues. Furthermore, it is essential that the prawn industry actively contributes towards the development of such designs so that they will be more readily accepted and adopted as part of commercial operations (Kennelly and Broadhurst, 1995).

In some prawn-trawl fisheries, industry has resisted gear modifications because of negative effects on gear performance (e.g. Renaud et al., 1993; Robins-Troeger et al., 1995). However, an inexpensive and simple modification that has been successfully tested and adopted in fish trawls in the North Atlantic involves changing only the configuration of mesh in the codend by hanging conventional diamond-shaped mesh on the bar (termed "square mesh") (e.g. Robertson and Stewart, 1988; Fonteyne and M'Rabet, 1992; Suuronen and Millar, 1992). Panels of square mesh have also been used successfully in prawn trawls to improve target-selectivity and to reduce the bycatch of juvenile fish. For example, in the Icelandic shrimp, *Pandalus borealis*, fishery, Thorsteinsson (1992) found that codends made entirely from square mesh effectively reduced the catches of small prawns (10–20% of catch) and 0-group gadoids. In New South Wales (NSW), Australia, Broadhurst and Kennelly (1996; 1997) showed that strategically located composite panels of square mesh (BRDs) in diamond-mesh codends effectively excluded large quantities of unwanted fish and there was no concomitant reduction in catches of the targeted prawns, *Penaeus plebejus*.

Through industry involvement in research, these sorts of results have facilitated the rapid endorsement and acceptance of designs in the respective fisheries and in some cases, in other fisheries sharing similar characteristics (e.g. similar gear configurations, target species, etc). An example of this type of transfer of technology recently occurred in the Gulf St. Vincent prawn-trawl fishery in South Australia. This fishery currently involves ten vessels targeting western king prawns, *Penaeus latisulcatus*; some legally retained bycatch comprising balmain bugs, *Ibacus* spp., and southern calamari, *Sepioteuthis australis* are also taken. Operators are restricted by means of a series of controls that include a minimum mesh opening of 45 mm in the codend and a limit of 34 nights of trawling each year. Although no formal studies have been undertaken to determine the selectivity of the conventional gear or to quantify bycatches, in recent years fishermen have suggested that the mesh size is too small and retains unacceptable proportions of juvenile prawns and fish. During the 1996–97 season, in an attempt to increase the mean sizes of prawns caught, fishermen designed and incorporated full square-mesh codends in all their trawls (see Fig. 1).

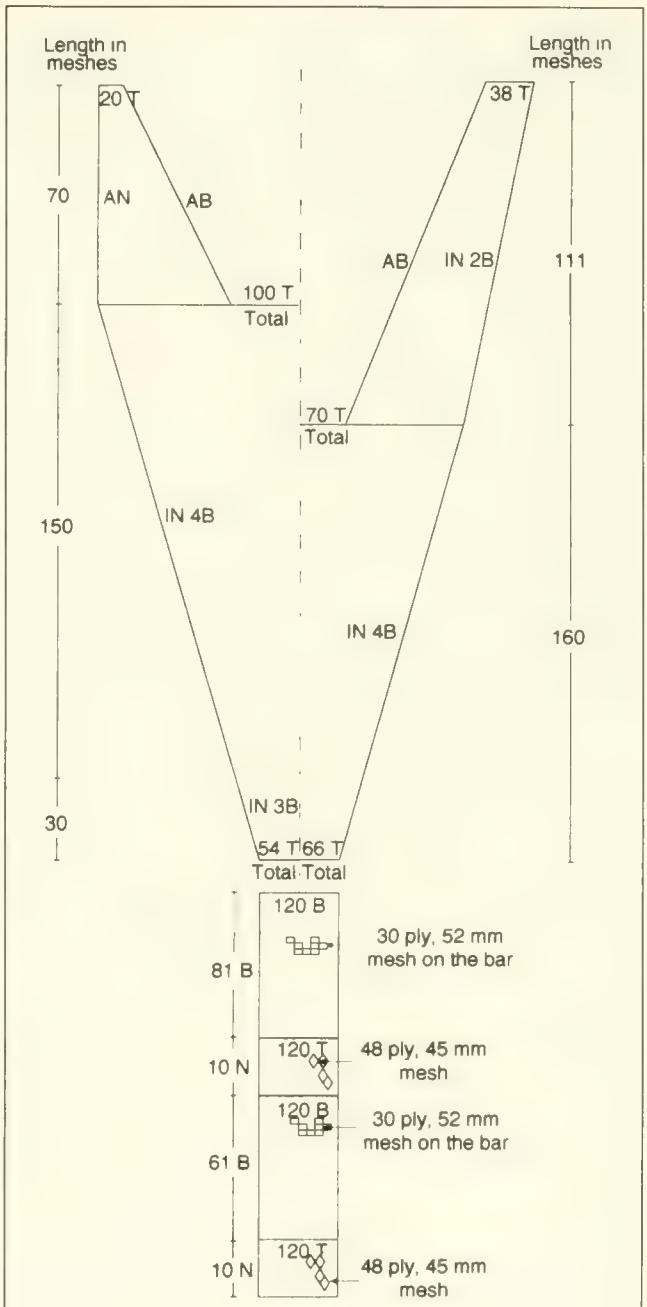

Figure 1

Diagrammatic representation of a "Gundry prawn trawl" and the industry developed "square-mesh-1 codend". T = transversals; N = normals; and B = bars.

Anecdotal reports from industry suggested that this codend (termed the "square-mesh-1 codend") re-

duced the bycatch of juvenile prawns and some small fish, although there were some concerns over suitable configurations of square mesh. Given that industry had already adopted the concept of using square mesh in codends, our aims in the present study were to modify the square-mesh-1 codend, after consultation with industry, so that it 1) incorporated a suitable BRD for unwanted fish and 2) increased the size-selectivity of targeted prawns.

Materials and methods

This study was done on commercial prawn-trawl grounds in Gulf St. Vincent, South Australia (Fig. 2), in November 1997, with a chartered commercial prawn-trawler (15 m). Three locally used prawn trawls (termed "Gundry trawls," Fig. 1), each with a headline length of 9.14 m were rigged in a standard triple gear configuration (see Andrew et al., 1991) and towed at 3 knots across a combination of sandy and light coral bottoms at depths ranging from 12 to 16.5 m. Each of the two outside trawls were rigged with zippers (Buraschi S-146R, pinlock sliders) to facilitate codend changes. The lengths of these zippers were calculated by assuming a fractional mesh opening of 0.35 (Broadhurst and Larsen, personal obs.) × the stretched mesh length × the mesh circumference. The middle net was not rigged in an identical manner to the outside trawls and therefore was excluded from any analysis.

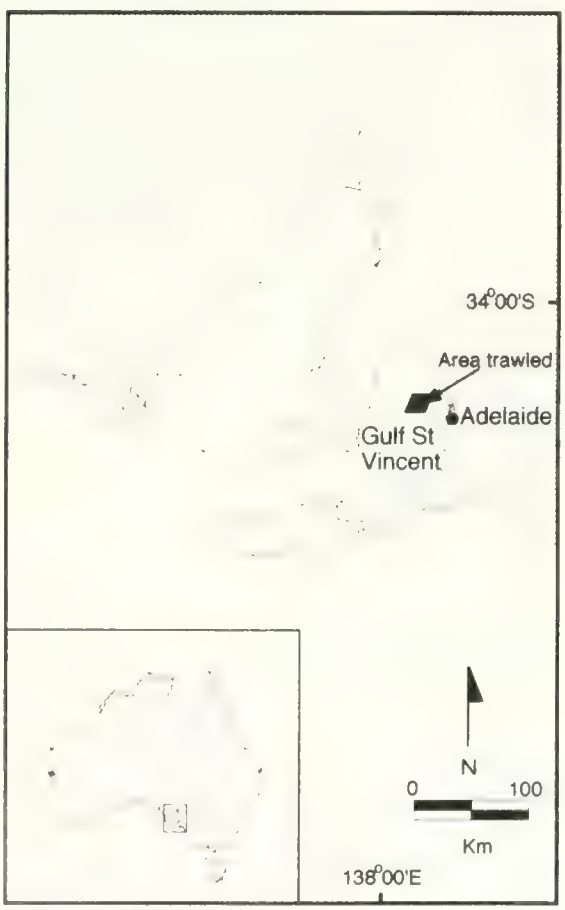

Figure 2
Location of Gulf St. Vincent and the area trawled.

Codends examined

Three codends, each attached to a zipper, were used in the experiment. The first codend, termed the control (Fig. 3A), represented conventional codends used prior to the 1996–97 fishing season and was made entirely of diamond-shaped meshes (45-mm mesh size, 2.35-mm diameter, 24-strand polyethylene twine), measuring 81 meshes in length and 100 meshes in circumference. The second and third codends (termed the composite-square-2 and composite-square-3 codends) comprised two sections of 52-mm mesh (400/36 ply, UV-stabilized, high-density polyethylene twine) cut on the bar. Each square-mesh section consisted of an upper and lower panel, sewn together so that knot directions were opposite. A panel of 85-mm netting (3-mm braided polyethylene twine), measuring 6 bars × 11 bars, was inserted into the tops of the posterior sections of each square-mesh codend starting approximately 1.1 m anterior to the last row of meshes (Fig. 3, B and C). This panel was positioned in a manner similar to that for the composite square-mesh panel used in NSW oceanic prawn trawls (see Broadhurst and Kennelly, 1996; 1997): that is, in an area of maximum displacement of water anterior to the end of the codend (to facilitate the escape of small fish, Broadhurst et al., 1999) but sufficiently in front of the anticipated build-up of catch.

The composite-square-2 codend comprised anterior and posterior square-mesh sections measuring 55 bars and 61 bars in length respectively. This codend was similar to the industry-developed square-mesh-1 codend, except that it had a circumference of 62 bars (1.6 m). The reduction in circumference from 120 bars (i.e. the industry design) to 62 bars was based on the expected fishing circumference of the normal diamond-mesh codend: that is, a fractional mesh opening (0.35) × the mesh size (45 mm) × the mesh circumference (100 T) = approx. 1.6 m. Two diamond-mesh 45-mm sections (mesh size, 400/48 ply UV-stabilized, high-density polyethylene twine), 10 meshes in length, and 100 meshes in circumference were inserted between the two square-mesh sections and immediately aft of the posterior square-mesh section (hanging ratio of 0.36) (Fig. 3B). The ante-

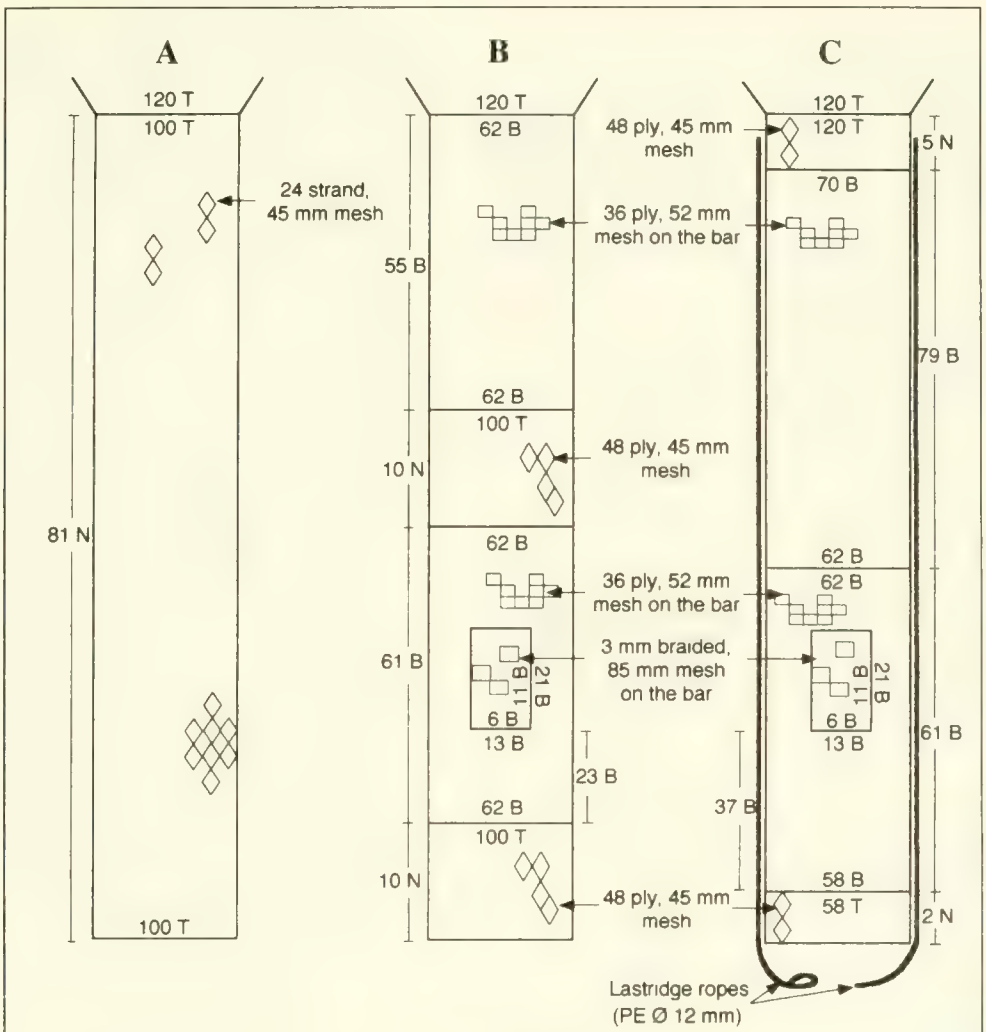

Figure 3

Diagrammatic representation of (**A**) the control codend, (**B**) composite-square-2 codend, and (**C**) composite-square-3 codend. T = transversals; N = normals; and B = bars.

rior diamond-mesh section was used to attach the codend lifting rope (termed "lazy-line"), whereas the posterior diamond-mesh section was used to attach the draw-string of the codend.

The composite-square-3 codend comprised an anterior square-mesh section 79 bars in length attached to a posterior square-mesh section 61 bars in length (Fig. 3C). The circumference of this codend tapered from 70 bars at the start of the anterior section to 58 bars at the end of posterior section. Two diamond-mesh sections (400/48 ply mesh size, UV-stabilized, high-density polyethylene twine), 2 meshes in length were attached immediately anterior and posterior (hanging ratio of 0.57) to the two square-mesh sections (Fig. 3C). The anterior diamond-mesh section measured 120 meshes in circumference, whereas the posterior diamond-mesh section measured 58 meshes in circumference and had the codend draw-string attached. Two 4.5-m lengths of 12-mm diameter, 3-strand polyethylene rope (termed "lastridge ropes") were firmly laced at a hanging ratio of approx. 0.9 to each of the two seams of the composite-square-3 codend to provide additional lengthwise strength to the entire codend. The posterior ends of the lastridge ropes extended past the codend and were secured together during each tow.

Sampling protocol and data collected

The two composite square-mesh codends were separately compared against the control codend. In each paired comparison, the control and composite square-mesh codend being tested were zipped to each outside trawl of the triple-rigged gear and towed simultaneously. The codends were used in normal com-

mercial tows of 45-min duration and randomly assigned after each tow (to eliminate biases between different trawls and sides of the vessel). The location of each tow was randomly selected from the available prawn-trawl locations that were possible under the fishing conditions. Over a total period of five nights, we initially completed 11 replicate tows of the composite-square-2 codend against the control. On the basis of results of this comparison and after discussions with representatives of industry, we then designed and constructed the composite-square-3 codend and immediately tested it against the control over another 11 replicate tows.

After each tow, the two codends were emptied onto a partitioned tray. Prawns and all individuals of commercially important species comprising bycatch were separated by species. The following categories of data were selected for each tow: the total weight of prawns and a subsample (100 prawns from each codend) of their lengths (to the nearest 1-mm carapace length); the total number of prawns (estimated from the weight of the subsample); the weights of total discarded bycatch, discarded noncommercial bycatch (i.e. species of no commercial value), and retained bycatch; the weights and numbers of commercially or recreationally (or both) important bycatch species; and the sizes (to the nearest 0.5 cm) of commercially or recreationally (or both) important fish. A random sample of prawns (approx. 14 kg) from each codend in each tow was separated and sent to A. Raptis & Sons PTY LTD (seafood processing plant) in Hindmarsh, Adelaide, where they were graded into commercial categories (number per pound) by a locally built automated "dynamic grading machine."

Several commercially important species were caught in sufficient quantities to enable meaningful comparisons. These were western king prawns, sand trevally, *Pseudocaranx wrighti*, red mullet, *Upeneichthys porosus*, school whiting, *Sillago bassensis*, Degen's leatherjacket, *Thamnaconus degeni*, southern sand flathead, *Platycephalus bassensis*, cuttlefish, *Sepia* spp., small-toothed flounder, *Pseudorhombus jenynsii*, and southern calamari.

Analysis of catch data

Data for all replicates that had sufficient numbers of each variable (defined as >2 individuals in at least 8 replicates) were analyzed with paired t-tests ($P \leq 0.05$). Except for the weights and numbers of prawns and small-toothed flounder, all variables were analyzed by using one-tailed tests of the hypothesis that the square-mesh codends caught less than the control. Although the composite square-mesh codends might have been expected to retain fewer prawns than the conventional diamond-mesh control codend (due to the larger square-shaped mesh), Broadhurst and Kennelly (1996; 1997) showed that trawls fitted with composite square-mesh panels caught more prawns than conventional trawls (possibly owing to a reduction in drag and a corresponding increase in swept area). Therefore, the weight and number of prawns were analyzed by using two-tailed tests. Catches of small-toothed flounder, a species that cannot pass through the square meshes, were also compared by using two-tailed tests. With the exception of data for catches of prawns, where analyses provided similar results for weights and numbers of variables, only data concerning numbers were included in Figure 4 to conserve space.

Size frequencies of commercially or recreationally (or both) important fish were plotted and compared with two-sample Kolmogorov-Smirnov tests (P=0.05), where there were sufficient data (n>25 in each codend, pooled across all tows).

Analysis of size-selectivity of prawns

The relatively large size of mesh used in the control (45-mm diamond mesh), compared with the composite square-mesh codends (52-mm mesh on the bar), meant that their selectivities overlapped. Insufficient numbers of smaller prawns were retained among individual hauls to enable analyses of between-haul variation (see Fryer, 1991). To provide sufficient data for analyses, size frequencies of prawns from each codend were combined across all tows. An estimated split model (Millar and Walsh, 1992) was used to fit logistic selection curves to these data by maximum likelihood method (Pope et al., 1975) by using the program "CC Selectivity" (Wileman et al., 1996). Logistic curve parameters, their standard errors, and 95% confidence limits were calculated for each codend. For each logistic curve, model deviance values were determined for a goodness-of-fit hypothesis (i.e. to test H_0: that the curves were logistic).

Size categories of commercially graded prawns from each codend were plotted and analyzed by using two-sample Kolmogorov-Smirnov tests (P=0.05). In these analyses, the numbers of prawns pooled across all samples from each codend were used for the degrees of freedom.

Results

Analysis of catch data

Compared with the control codend, both the composite-square-2 and composite-square-3 codends signifi-

cantly reduced the numbers of prawns caught (means reduced by 8.7% and 12.1%, respectively), with no significant reduction in weights (although the means were reduced by 1.8% and 3.7%, Fig. 4, A–B; Table 1). The weights of total discarded bycatch and discarded noncommercial bycatch were significantly reduced by 67.7% and 69.0%, respectively, in the composite-square-2 codend, whereas the composite-square-3 codend reduced these amounts by 58.4% and 54.2%. respectively (Fig. 4, C–D; Table 1). Both composite square-mesh codends significantly reduced the numbers and weights of sand trevally (by between 68.0% and 76.6%), red mullet, (by between 87.2% and 96.9%), school whiting (by between 90.6% and 96.9%), and southern sand flathead (by between 57.0% and 84.9%) (Fig. 4, E–H; Table 1). The composite-square-2 codend significantly reduced the mean number and weight of Degen's leatherjacket caught by 31.8% and 23.4%, respectively, and although not significant, these amounts were reduced by 24.6% and 20.8%, respectively, in the composite-square-3 codend (Fig. 4I; Table 1). There was also a significant reduction in the numbers of retained southern calamari, by 33.9% in the composite-square-3 codend (Fig. 4J; Table 1).

Two-sample Kolmogorov-Smirnov tests comparing the size-frequency distributions for fish measured from the control and composite square-mesh codends showed significant differences in the relative size compositions of sand trevally retained by both composite square-mesh codends and red mullet retained by the composite-square-2 codend (the control codend retained proportionally more larger fish, Fig. 5, A–B). No significant differences were detected in the size compositions of Degen's leather jacket retained in the composite square-mesh and control codends (Fig. 5C). There were insufficient data to analyze size-frequency distributions of school whiting and southern sand flathead.

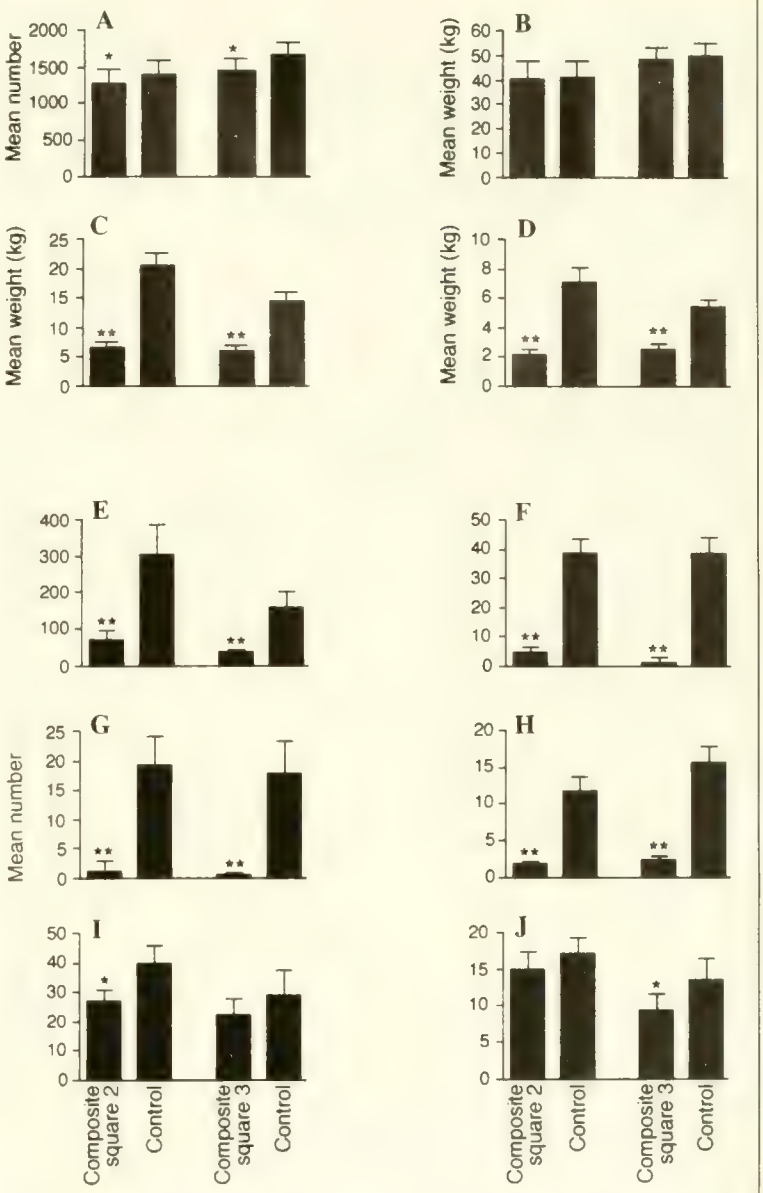

Figure 4

Differences in mean catches (per 45-min tow ± SE) between the composite square-mesh codends and control codend: the (**A**) numbers and (**B**) weights of king prawns (*Penaeus latisulcatus*); the weights of (**C**) total discarded bycatch and (**D**) discarded noncommercial bycatch; and the numbers of (**E**) sand trevally (*Pseudocaranx wrighti*), (**F**) red mullet (*Upeneichthys porosus*), (**G**) school whiting (*Sillago bassensis*), (**H**) southern sand flathead (*Platycephalus bassensis*), (**I**) Degen's leather jacket (*Thamnaconus degeni*), and (**J**) southern calamari (*Sepioteuthis australis*). ** = significant ($P<0.01$); * = significant ($P<0.05$).

Analysis of size-selectivity of prawns

The raw data, observed selectivity, and calculated logit values for prawns captured in the codends are listed in Table 2. Figure 6 shows the corresponding logistic length selection curves derived for each composite square-mesh codend. Model deviance indicated sufficient goodness of fit for both of these selection curves (Table 3; Fig. 7) although some size classes

Table 1

Summaries of paired *t*-tests comparing composite square-mesh and control codends. Weights and numbers of prawns and small-toothed flounder were analyzed with a two-tailed paired *t*-tests, whereas the remaining variables were analyzed with one-tailed paired *t*-tests. *n* = number of replicates; disc = discarded; noncomm = noncommercial. Significant *P*-values are in bold.

	Composite-square-2 versus control			Composite-square-3 versus control		
	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*
No. of prawns	2.574	**0.027**	11	2.853	**0.017**	11
Wt. of prawns	0.648	0.531	11	0.915	0.382	11
Wt. of total disc bycatch	6.521	**0.0001**	11	6.662	**0.0001**	11
Wt. of disc noncomm bycatch	5.251	**0.0002**	11	6.051	**0.0001**	11
Wt. of retained bycatch	–0.424	0.659	11	0.947	0.183	11
No. of sand trevally	3.345	**0.003**	11	3.719	**0.002**	11
Wt. of sand trevally	4.016	**0.001**	11	4.050	**0.001**	11
No. of red mullet	6.901	**0.0001**	11	6.728	**0.0001**	11
Wt. of red mullet	6.927	**0.0001**	11	8.033	**0.0001**	11
No. of school whiting	6.912	**0.0001**	11	5.111	**0.0003**	10
Wt. of school whiting	4.887	**0.0003**	11	4.896	**0.0004**	10
No. of Degen's leatherjacket	2.442	**0.017**	11	1.378	0.099	11
Wt. of Degen's leatherjacket	1.945	**0.040**	11	1.139	0.140	11
No. of southern sand flathead	5.470	**0.0002**	11	6.328	**0.0001**	11
Wt. of southern sand flathead	5.487	**0.0002**	11	3.585	**0.0025**	11
No. of cuttlefish	1.247	0.122	10	1.037	0.163	10
Wt. of cuttlefish	1.217	0.127	10	0.792	0.224	10
No. of small-toothed flounder	–0.882	0.407	8	1.537	0.163	9
Wt. of small-toothed flounder	0.940	0.378	8	0.208	0.779	9
No. of southern calamari	0.772	0.229	11	3.123	**0.005**	11
Wt. of southern calamari	–0.576	0.711	11	–0.179	0.568	11

had high deviance residuals (Fig. 7, see also Appendix). Although all selectivity parameter estimates were slightly greater in the composite-square-3 codend, the 95% confidence limits for these estimates indicated that there were no statistically significant differences between the two modified codends.

Two-sample Kolmogorov-Smirnov tests comparing the commercial size compositions of prawns retained in each codend showed significant differences between the composite square-mesh and control codends (Fig. 8). Both composite square-mesh designs caught proportionally more larger prawns (<9/12 per pound) and fewer smaller individuals (>16/20 per pound).

Discussion

The work described in this paper illustrated the effectiveness of a strategically located panel of square mesh in codends for reducing catches of juvenile fish (see also Robertson and Stewart, 1988; Fonteyne and M'Rabet, 1992; Briggs, 1992; Broadhurst and Kennelly, 1996, 1997) and quantified, for the first time in commercial penaeid prawn-trawls, the utility of large panels of square mesh for improving the size-selectivity of the targeted prawns.

The composite square-mesh codends were equally effective in excluding large quantities of small individuals of fusiform species, including sand trevally, red mullet, school whiting, and southern sand flathead and there was no significant reduction in weights of prawns or total retained bycatch (Fig. 4; Table 1). Although the square mesh used throughout the main sections of both codends may have been large enough to permit some smaller fish (e.g. red mullet) to escape, the differences in the sizes of many fish retained between the composite square-mesh codends and the control (Fig. 5) indicated that to achieve the significant and quite large reductions in catch, most fish probably escaped through the larger 85-mm mesh panel located in the tops of the posterior sections of the codends.

The escape of large numbers of these individuals through the 85-mm square-mesh panel in both codends may be attributed to the influences of water

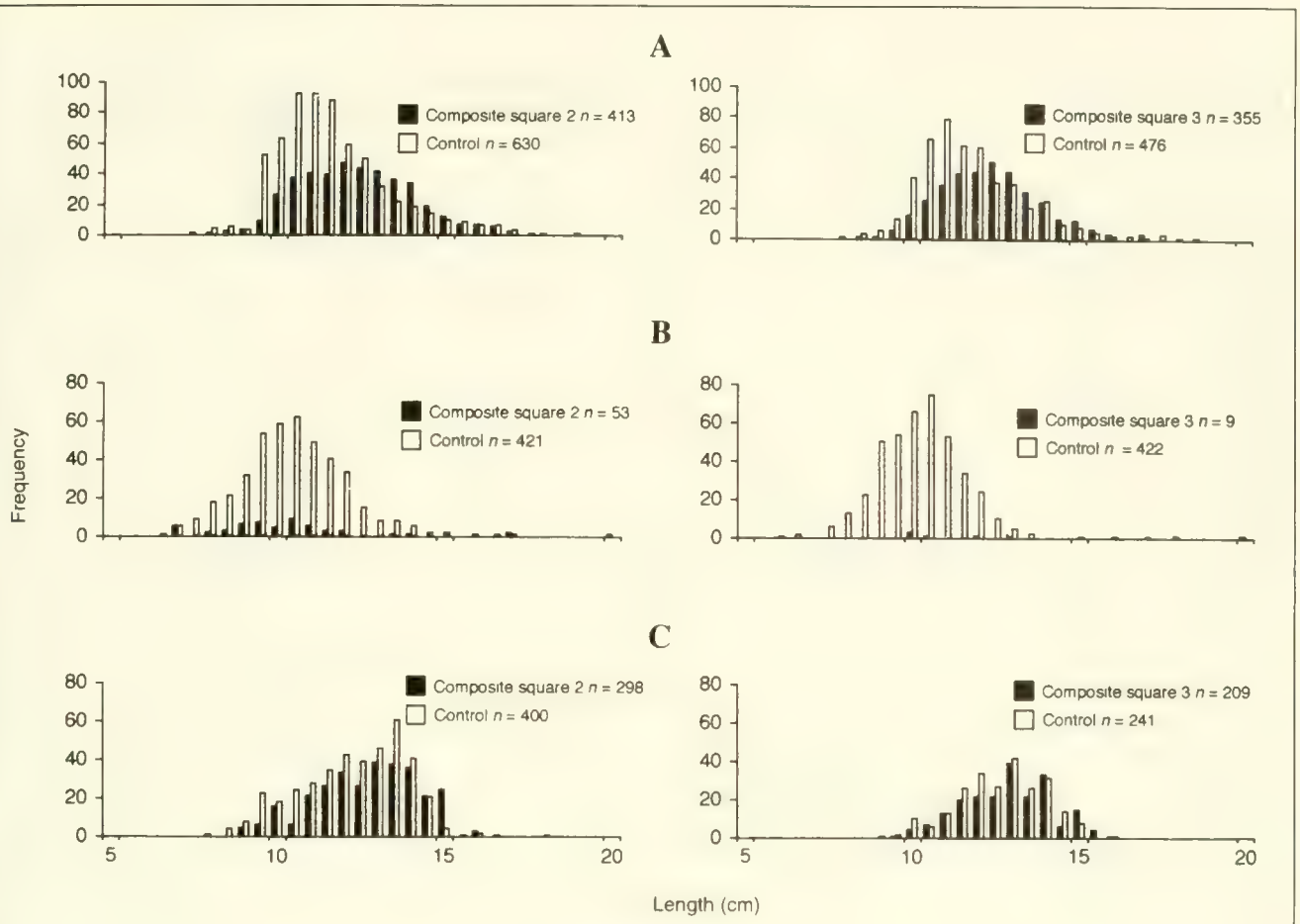

Figure 5

Size-frequency distributions of the composite square-mesh codends and control codend for (**A**) sand trevally (*Pseudocaranx wrighti*), (**B**) red mullet (*Upeneichthys porosus*), (**C**) Degen's leatherjacket (*Thamnaconus degeni*), (**D**) school whiting (*Sillago bassensis*), and (**E**) southern sand flathead (*Platycephalus bassensis*).

flow anterior to the catch. The location of the panel (approx. 1.1 m from the end of the codend, Fig. 3) was based on a similar design (termed the composite square-mesh panel) that is currently used commercially in oceanic prawn trawls in NSW where it has been shown to be very effective in reducing the bycatch of large numbers of small fish (Broadhurst and Kennelly, 1996, 1997). In previous experiments, Broadhurst and Kennelly (1996) and Broadhurst et al. (1999) determined that at this position, there is some displacement of water forwards owing to the twine area and build-up of catch in the posterior section of the codend. Because small fish are probably using anaerobic muscle power to maintain position in the moving trawl and are quite fatigued when they enter the codend, this displaced water may be sufficient 1) to assist them to swim forwards and out through the larger meshes in the panel; and (or) 2) to enable them to reduce their tail-beat frequencies and maintain their position in the vicinity of the larger mesh for a longer period, increasing their chances of randomly escaping. The extent to which such a flow facilitated the escape of fish in the present study probably depended on their relative size or physiology (or both), because these factors largely influence swimming speed and endurance (Beamish, 1978). For example, the bycatch of fast-swimming species, such as sand trevally, and relatively large individuals of school whiting and southern flathead was greatly reduced in the two modified designs. However, although statistically significant, there was only a 30% reduction in the numbers of the relatively small Degen's leather jackets in the composite-square-2 codend and a lower nonsignificant 24% reduction in the composite-square-3 codend (Fig. 4I; Table 1).

A possible explanation for the significant reduction of Degen's leather jacket from the composite-square-2 codend may be the configuration of mesh

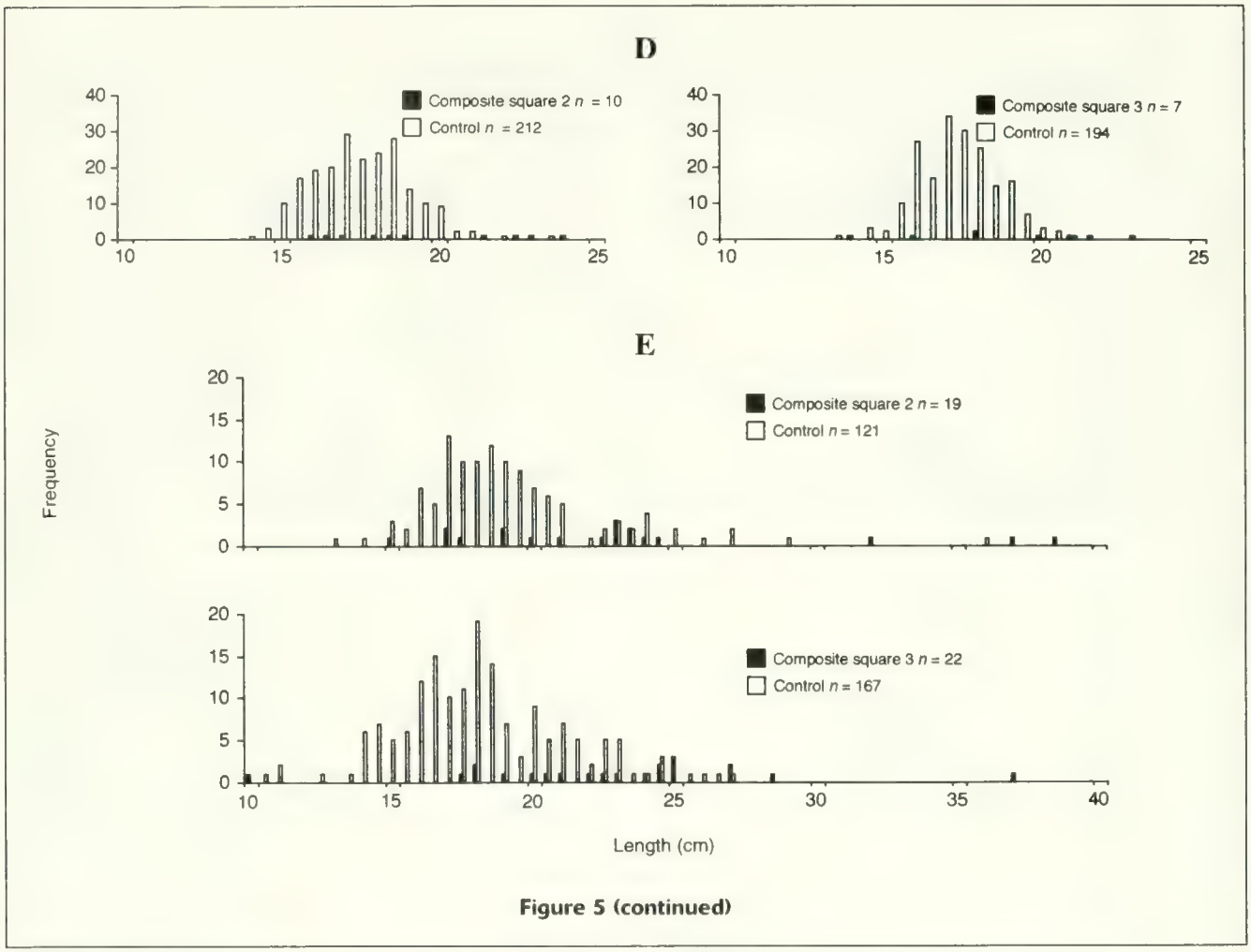

Figure 5 (continued)

used in the posterior section of the codend and the effects that this had on distribution of catch and water flow. Because the posterior diamond-mesh section in this codend was 10 meshes in length, 100 meshes in circumference, and attached to a square-mesh section 62 bars in circumference (hanging ratio of 0.36), as the catch increased it would have spread laterally, increasing its surface area that was incidental to the flow and, therefore, increasing the displacement of water forwards (see Broadhurst and Kennelly, 1996, 1999). The composite-square-3 codend, however, was designed to increase size-selectivity of prawns and was tapered to a circumference of 58 bars attached to a posterior diamond-mesh section that was 2 meshes in length and only 58 meshes in circumference (hanging ratio of 0.57). Combined with lastridge ropes, this configuration would have forced a much smaller codend diameter than in the composite-square-2 codend, restricting any lateral distribution of catch. Any consequent reduction in surface area that was incidental to the flow and displacement of water forwards in this codend (which would limit any assistance to swimming fish) may account for the nonsignificant reduction of Degen's leather jackets and the poorer exclusion of small individuals comprising discarded noncommercial bycatch (Fig. 4D). It should be noted, however, that these results were based on only 11 tows and that further experiments may be required to provide additional evidence to either support or refute the hypothesis discussed above.

Although the mesh configuration and water flow in the composite-square-2 codend may have contributed to the escape of slightly more fish, in terms of optimizing sizes of prawns retained, the composite-square-3 codend appeared to be a better design. Although the 95% confidence limits about the selectivity parameters indicated no significant differences between the two designs (Fig. 6; Table 3), there was some evidence to suggest that the composite-square-3 codend did appear to select slightly more commercial-size prawns. For example, compared with the control, this codend caught significantly fewer prawns by number (difference between means of

Table 2

Length-frequency distributions (pooled across all tows) for prawns captured in the composite square-mesh and control codends, the observed selectivity (ratio of catches), and the fitted logit values. Carapace length in mm; CS2 = composite-square-2 codend; CS3 = composite-square-3 codend.

Carapace length	CS2 codend	Control codend	Observed selectivity	Logit value	CS3 codend	Control codend	Observed selectivity	Logit value
15	0	0	0.00	0.019	0	0	0.00	0.002
16	0	2	0.00	0.025	0	0	0.00	0.003
17	0	0	0.00	0.032	0	0	0.00	0.005
18	0	0	0.00	0.041	0	2	0.00	0.007
19	0	3	0.00	0.052	0	2	0.00	0.009
20	0	3	0.00	0.066	0	2	0.00	0.013
21	0	5	0.00	0.084	0	4	0.00	0.019
22	1	10	0.10	0.106	0	11	0.00	0.026
23	2	7	0.28	0.133	0	7	0.00	0.036
24	0	4	0.00	0.165	0	10	0.00	0.050
25	1	4	0.25	0.204	2	5	0.40	0.068
26	1	6	0.17	0.249	1	8	0.12	0.093
27	4	10	0.40	0.301	0	0	0.00	0.126
28	6	8	0.75	0.357	1	7	0.14	0.169
29	5	10	0.50	0.418	1	2	0.50	0.222
30	10	13	0.77	0.482	4	16	0.25	0.285
31	18	27	0.67	0.546	8	25	0.32	0.359
32	34	42	0.81	0.609	24	27	0.89	0.440
33	43	56	0.77	0.668	48	48	0.10	0.525
34	60	77	0.78	0.723	61	74	0.82	0.608
35	87	96	0.91	0.771	76	112	0.68	0.685
36	116	125	0.93	0.813	105	147	0.71	0.753
37	109	98	1.11	0.849	118	111	1.06	0.811
38	81	77	1.05	0.879	92	62	1.48	0.857
39	60	57	1.05	0.904	63	51	1.23	0.894
40	58	49	1.18	0.924	66	44	1.50	0.922
41	48	48	1.00	0.940	62	49	1.26	0.943
42	53	57	0.93	0.953	63	56	1.12	0.959
43	56	55	1.02	0.964	76	50	1.52	0.970
44	44	39	1.13	0.972	57	46	1.24	0.979
45	31	33	0.94	0.978	32	41	0.78	0.985
46	26	23	1.13	0.983	33	30	1.10	0.989
47	33	18	1.83	0.987	34	18	1.89	0.992
48	33	21	1.57	0.989	29	20	1.45	0.994
49	15	25	0.60	0.992	14	16	0.87	0.996
50	17	10	1.70	0.994	17	9	1.89	0.997
51	13	7	1.86	0.995	12	10	1.20	0.998
52	8	3	2.67	0.996	7	7	1.00	0.999
53	9	2	4.50	0.997	1	5	0.20	0.999
54	9	2	4.50	0.998	2	1	2.00	0.999
55	2	1	2.00	0.998	5	4	1.25	0.999
56	2	2	1.00	0.999	5	3	1.66	0.999
57	4	7	0.57	0.999	2	3	0.67	0.999
58	1	1	1.00	0.999	1	0	0.00	0.999
59	2	0	0.00	0.999	0	1	0.00	0.999
60	0	0	0.00	0.999	1	0	0.00	0.999
61	0	0	0.00	0.999	1	1	1.00	0.999

Table 3

Computed selectivity parameters for prawns (carapace length in mm) from the two composite square-mesh codends and deviance values for logistic curve goodness-of-fit. Standard errors are given in parentheses. a, b = logistic parameters (Pope et al., 1975). P = split proportion from estimated split model (Millar and Walsh, 1992).

	Composite-square-2 codend		Composite-square-3 codend	
a	−7.803		−11.079	
b	0.257		0.338	
P	0.544		0.562	
		95% confidence limits		95% confidence limits
25% retention (L_{25})	26.02 (1.19)	20.14–30.94	29.46 (0.76)	25.42–33.07
50% retention (L_{50})	30.28 (1.19)	28.13–33.38	32.71 (0.82)	31.29–34.59
75% retention (L_{75})	34.56 (1.76)	29.73–42.20	35.95 (1.13)	32.38–40.91
Selection range (SR)	8.53 (0.6)	4.89–12.16	6.49 (0.5)	4.21–8.76
Deviance	32.48		46.54	
df	39		40	
P-value	0.760		0.221	

12.1%) than did the composite-square-2 codend (difference between means of 8.1%), and there was no significant reduction in weights (Fig. 4; Table 1).

These slight differences in size-selectivity of prawns may be explained in terms of the behavior of prawns in the codend and the different configurations of mesh discussed above. Previous studies have shown that the response of prawns to stimuli from the trawl is minimal and after initial contact with the leading edge of the footrope, the prawns are quickly forced into the rear of the codend (Lochhead, 1961; Watson, 1976). Their escape at this point is primarily determined by their probability of randomly encountering openings between meshes that are large enough to pass through. In the composite-square-2 codend, the hanging ratio between the posterior diamond and square-mesh sections would have restricted the fractional diamond-mesh openings, limiting the opportunity for escape. Further, as the catch increased and spread laterally, this would have widened the diameter of the posterior section, providing prawns with less opportunity of encountering any open meshes in the sides of the codend. In contrast, we designed the composite-square-3 codend, so that it would assume a smaller diameter and circumference during fishing, but with a greater area of square mesh, thereby providing more opportunity for prawns to randomly encounter the sides of the codend and the open square meshes.

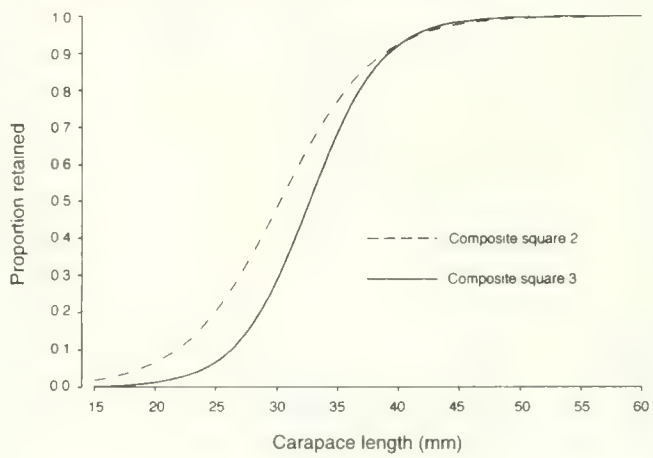

Figure 6

Size-selectivity curves for king prawns (*Penaeus latisulcatus*) from the composite square-mesh codends.

The results obtained in this study showed that composite square-mesh codends in penaeid prawn trawls can improve size-selectivity of the targeted prawns while reducing large quantities of unwanted fish. It is also apparent, that such modifications may improve the overall efficiency of the trawl in terms of increasing catches of prawns. For example, although the composite-square-2 and square-3 codends significantly reduced the numbers of prawns caught by 8.7% and 12.1%, compared with the control, the differences in weights of prawns were much smaller, to the point where they were nonsignificant (e.g. 1.8% and 3.7%, respectively). To achieve such a result, the two trawls containing composite square-mesh codends caught more prawns but retained mainly larger-size individuals.

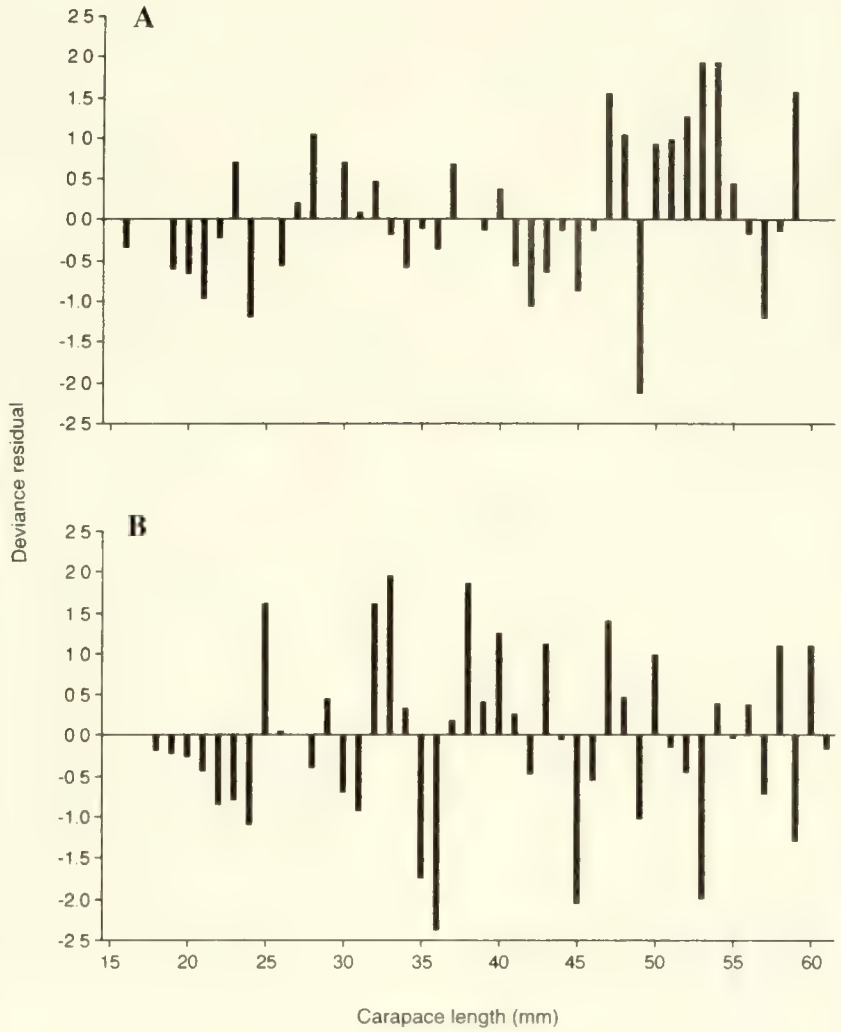

Figure 7

Plots of the deviance residuals from selection curves for the (**A**) composite-square-2 codend and (**B**) composite-square-3 codend.

One hypothesis to explain this result is that the large, open, square meshes in the composite square-mesh codends, combined with the overall size of the codends (approx. 4 m in length) allowed a faster release of water from the body of the trawl than did the control. Such an increase in flow may have resulted in prawns quickly passing into the codend after initial contact with the footrope, with less chance of randomly escaping over the headrope or out through the mouth of the trawl. In support of this, Walsh et al., (1992) provided evidence of similar flow-related effects on the catches of fish (American plaice, *Hippoglossoides platessoides*) from trawls fitted with square-mesh codends. In the present study, however, any potential effects of increased flow did not appear to influence fish such as small-toothed flounder (the only species that could not pass through the square mesh), because there were no significant differences in the catches between the composite square-mesh and control codends (Table 1). An alternative hypothesis proposed by Broadhurst and Kennelly (1997) to describe a similar increase in catches of prawns from NSW oceanic prawn trawls containing codends with composite square-mesh panels is that by reducing the weight of bycatch and therefore the drag in the codend, trawls with the composite square-mesh achieved slightly more swept area than did controls, thereby covering more of the sea bed and capturing more prawns.

Regardless of the underlying mechanisms, the increase in catches of target-size prawns, combined with the substantial reductions in the bycatch of fish,

led to unanimous industry acceptance and adoption of the composite-square-3 codend within two weeks of the conclusion of the field work described in this paper. Fishermen have since reported that the codend has minimal distortion (due to the lastridge ropes), allows increased tow duration, and provides an improved quality of prawns. These results illustrate the benefits that can be derived through liaison with industry and by incorporating their ideas into modifications to improve the selectivity of prawn trawls. Such voluntary adoption should ensure the continued development and refinement of designs, as part of normal commercial operations.

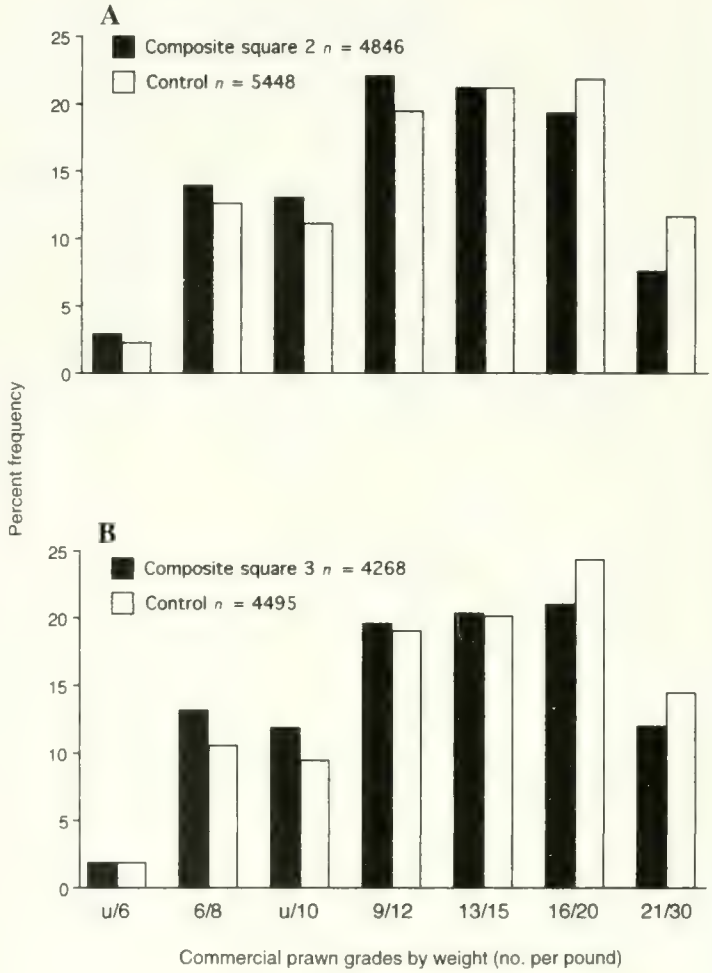

Figure 8

Commercial size categories of king prawns (*Penaeus latisulcatus*) caught with the (**A**) composite-square-2 and control codends and (**B**) composite-square-3 and control codends (u=under).

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Appendix

The plots of deviance residuals (Fig. 7) for both selection curves provided in Figure 6 showed that most of the size classes of prawns above 45-mm carapace length had high deviances. By removing these data from analysis and also the frequencies for the 35- and 36-mm size classes from the composite-square-3 codend, the *P*-values for model goodness-of-fit increased from 0.760 to 0.999 for the composite-square-2 codend (df=25) and from 0.221 to 0.853 for the composite-square-3 codend (df=21) (Table 4). Although this alternative analysis does provide selectivity parameters that are slightly different from those calculated in Table 3, the overall interpretation of the data remains the same.

Table 4

Computed selectivity parameters for prawns (carapace length in mm) from the two composite square-mesh codends and deviance values for logistic curve goodness-of-fit, excluding all entries above 45-mm carapace length for both codends and the 35- and 36-mm size classes from the composite-square-3 codend. Standard errors are given in parentheses. a, b = logistic parameters (Pope et al., 1975). P = split proportion from estimated split model (Millar and Walsh, 1992).

	Composite-square-2 codend		Composite-square-3 codend	
a	−9.556		−13.58	
b	0.330		0.424	
P	0.513		0.573	
		95% confidence limits		95% confidence limits
25% retention (L_{25})	25.59 (0.60)	21.80–29.17	29.46 (0.59)	26.33–32.38
50% retention (L_{50})	28.92 (0.63)	27.73–30.42	32.05 (0.66)	30.90–33.67
75% retention (L_{75})	32.24 (0.92)	28.68–36.64	34.64 (0.96)	31.77–38.67
Selection range (SR)	6.65 (0.92)	4.84–8.45	5.18 (0.81)	3.42–6.95
Deviance	7.91		14.75	
df	25		21	
P–value	0.999		0.853	

Morphometric criteria for estimating sexual maturity in two snappers, *Etelis carbunculus* and *Pristipomoides sieboldii*

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Abstract.—A gross measure of reproductive condition (ovary weight adjusted for body size and oocyte volume) is developed and evaluated as an alternative to commonly used gonad indices, for classifying the maturity status of individual ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*), two species of eteline snappers (Lutjanidae) that contribute to the deep-slope handline fishery in Hawaii. Discriminant analysis and logistic regression, based on body length, ovary weight, and oocyte volume, were used to classify fish as either immature or mature. Discriminant analysis correctly classified the maturity of about 98% of both ehu and kalekale, with histological criteria as the standard for comparison. Logistic regression correctly classified maturity of 97% of the ehu and 100% of the kalekale. Misclassification errors increased by 3.75–5% (discriminant analysis) or 0–5% (logistic regression) if oocyte volume was excluded and only body length and ovary weight were used as predictors of maturity.

For kalekale, estimates of lengths at which 50% are sexually mature (L_{50}) were identical (29.0 ±1.8 [SE] cm fork length, FL; r^2=0.92), when maturity was classified histologically or by logistic regression on body, ovary, and oocyte metrics. For ehu, L_{50} estimates were similar (r^2=0.96) for maturity assignments based on histology (27.9 ±2.4 cm FL) and on logistic regression using gross metrics (27.8 ±2.3 cm FL).

We conclude that gross morphometrics can provide adequate proxies for histological evidence when categorizing sexual maturity in asynchronous, multiple-spawning fishes like eteline lutjanids. The potential benefits of using gross metrics for assessing sexual maturity in other serial spawners are briefly discussed.

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Body size at sexual maturity is of fundamental importance in fishery stock assessment (e.g. when calculating a "spawning potential ratio" [SPR, Goodyear, 1993; Somerton and Kobayashi[1]]). In fisheries applications, average size at maturity is usually expressed as the body length at which 50 percent of females are mature (L_{50}), and is typically estimated by fitting a model such as the logistic (Gunderson et al., 1980; O'Brien et al., 1993) to observed percentages of mature fish within several length classes. Estimating percentage mature by size class assumes that individuals can be accurately classified as either immature or mature.

Various methods have been used to classify individual female fish as sexually mature, including gross inspection of ovaries, light microscopic examination and measurement of whole oocytes in fixed tissue samples, histological stains of intraovarian inclusions, and an array of ratios, commonly referred to as "gonad indices" or "gonadosomatic indices" (GSIs) that standardize gonad mass to body size. These methods differ in precision, accuracy, and processing time. Gross inspection of ovaries is quick but highly subjective and often cannot be used to distinguish between immature and spent (resting) mature fish (West, 1990). Light microscopy of whole oocytes can effectively identify the most advanced oocyte mode only if the dynamics of oocyte growth are known for the particular species and may be inaccurate for ovaries that also contain oocytes in intermediate stages of vitellogenesis (West, 1990). Histological staining of tissue samples for detection of cytoplasmic inclusions (yolk, oil globule presence and number) in the most advanced oocytes provides the best evidence of maturation and is the most accurate method, but it is also the most time consuming and expensive (Delahunty and deVlaming, 1980).

Usually only a single method has been used in a given study, although some studies (e.g. Cayre and Laloe, 1986; Hay et al., 1987; Kjesbu, 1991; Olsen and Rulifson, 1992; Ramsay and Witthames, 1996) have at least attempted to confirm maturity classifications with more than one technique. Average size at maturity has usually (e.g. Higham and Nicholson, 1964; DeMartini and Fountain, 1981), but not always (Erickson et al., 1985a; Matsuyama et al., 1987; McQuinn, 1989; Hunter et al., 1992;

[1] Somerton, D. A., and D. R. Kobayashi. 1990. A measure of overfishing and its application on Hawaiian bottomfishes. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Sci. Cent. Admin. Rep. H-90-10, 18 p.

Render et al., 1995), been identified subjectively if more than one method of classification was used, sometimes with inconsistent results (Trippel and Harvey, 1991). Recently, West (1990) identified microscopic staging coupled with a gonad index as the most objective and quantitative method.

Gonad indices should be used with caution as measures of sexual maturity and require biologically realistic companion analyses (e.g. Koya et al., 1995). A fundamental flaw of ratios, such as gonad indices, is that they either lose or obscure meaningful information in the numerator and denominator of the ratio (Garcia-Berthou and Moreno-Amich, 1993). Gonad indices also are questionably applicable for asynchronous, multiple-spawning fishes (deVlaming et al., 1982). There are two major reasons for this. First, because multiple-spawners ripen and shed numerous batches of eggs, the ovary weight of an individual fish fluctuates cyclically and often greatly during the spawning season. Second, somatic weight often varies independently of ovary weight for individuals. Somatic "condition" (robustness) usually declines monotonically, and sometimes greatly, as somatic energy reserves become progressively depleted over the spawning season, whereas ovary weights cycle high and low as the individual continues to spawn (Delahunty and deVlaming, 1980; deVlaming et al., 1982). Variances in GSIs among mature fish are unavoidably large (e.g. Macer, 1974) because small, ready-to-spawn fish sometimes have higher GSIs than larger fish that have just shed their eggs. Other potential complications include differences in ovarian cycling frequencies (spawning intervals) between small and large females within populations (Hunter and Macewicz, 1985). Thus even refinements of the conventional GSI such as the "relative gonadal index" (RGI) of Erickson et al. (1985b), in which gonadal investment is adjusted for size allometry, can be inappropriate for asynchronous, multiple-spawners if the dynamics of somatic and gonadal condition are unknown. Statistical descriptors of sexual maturity that are more accurate and robust than GSIs need to be developed (Garcia-Berthou and Moreno-Amich, 1993; Winters and Wheeler, 1996; Jons and Miranda, 1997).

Our study has several complementary objectives. First, we evaluate four gross metrics (fish body length and weight, ovary weight, and oocyte size) for describing stages of sexual maturation in two eteline lutjanids (ehu, *Etelis carbunculus*, and kalekale, *Pristipomoides sieboldii)* that contribute to the deep-slope bottom fishery in Hawaii. We examine these four characters because they are readily measured and less costly than the more accurate histological staining of ovarian tissue. We also independently assess stage of sexual maturity for each species based on histology of ovarian tissue samples from specimens collected during peak periods of spawning. In our study, we use discriminant analysis and logistic regression to further classify individual fish as either immature or mature on the basis of gross morphometric and histological criteria. In conclusion, we evaluate the results of gross classifications of maturity for ehu and kalekale by assessing how well L_{50} estimates based on statistical assignments of maturity with gross metrics agree with L_{50} estimates based on histological evidence of maturity.

Materials and methods

Fish collection and shipboard processing

Two types of fish collections were used: hook and line and bottom trawling. For exploitable-sized fish of both species, hydraulic handline gurdies with sizes 28 and 34 Izuo circle hooks (baited with squid strips) were used to fish near bottom at depths of 60–300 m, on insular slopes and submerged banks located between 22–25°N lat. and 160–170°W long. in the Northwestern Hawaiian Islands (NWHI). Specimens were collected in September 1992; during June, July, August, and September 1993; in August 1996, and in July and August 1997 (Table 1). Most line-fishing was conducted during daylight hours (0730–1930) aboard the NOAA ship *Townsend Cromwell.* Additional small kalekale were sampled at 60–65 m off south Molokai, Main Hawaiian Islands, during August 1992 and September 1993. We also examined additional small ehu caught by bottom trawl at 88–97 m near Kure Atoll (NWHI) in early June 1977 (Table 1). All specimens examined were collected during the protracted summer spawning period of eteline snappers in Hawaiian waters (Ralston, 1981; Everson, 1984; Everson et al., 1988). Ehu are thought to be serial spawners (Everson, 1984), and oocyte size distributions within ovaries suggest that Hawaiian populations of both species comprise asynchronous spawners.[2]

Once captured, fish were placed immediately on ice. Within an hour of capture, fork length (FL) to the nearest 0.1 cm and ovary-free body weight (OFBW, in g) was estimated for each fish.

Ovary weight (OW) of each specimen that appeared female was estimated ±0.1 g (if <5g), ±1 g (if 5–100 g) and ±10 g (if >100 g). A tissue plug (1–50 g, de-

[2] 1994. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Unpubl. data.

Table 1

Summary statistics for ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*) used in analyses. Months were sampled in the years 1992, 1993, 1996, and 1997. FL = fork length; OFBW = ovary-free body weight; OW = ovary weight.

		FL (mm)		OFBW (g)		OW (g)		
Species	Month	Median	Min–Max	Median	Min–Max	Median	Min–Max	*n*
Ehu	Jun–Jul	368	91–551	865	15–2984	10	0.1–136	37
	Aug	356	203–544	826	200–3260	24	0.3–350	80
	Sep	370	270–595	894	351–3615	28	3.0–200	64
	Total	362	91–595	850	15–3615	23	0.1–350	181
Kalekale	Jun–Jul	340	334–390	714	596–1054	40	26–46	5
	Aug	340	156–438	626	51–1400	20	0.1–120	51
	Sep	363	150–412	846	51–1247	17	0.1–39	24
	Total	348	150–438	710	51–1400	20	0.1–120	80

pending on ovary size, and including the ovarian wall) was taken from the central one-third of either the right or left ovary (random choice) and placed in 10% formalin sea-water.

Laboratory processing

Most ovary specimens were processed within 1–2 months after collection. Diameters of 25 of the largest viable oocytes were then measured (random axis, 63× magnification) for each specimen with a dissecting microscope. The median of 25 diameters provides a cost-efficient estimator of average maximum oocyte size for ehu (Lau and DeMartini, 1994).

For each preserved ovary specimen, a subsample of the ovary was dehydrated, imbedded in paraffin, and a minimum of three sections was cut (at 6 μm) and stained with Harris's hematoxylin, followed by eosin counterstain (Hunter and Macewicz, 1985). Slide sections were examined with a compound microscope at 40–500× for the presence and relative quantity of eosinophilic yolk (unyolked oocytes: class 1 of Murphy and Taylor, 1990; partly yolked: classes 2–3; yolked: classes ≥4). If oocytes were yolked, we further noted the presence of postovulatory follicles (POF: class 6), hydrating or hydrated oocytes (HYD: class 7), and oocytes undergoing α or β atresia (class 8: Murphy and Taylor, 1990). Individuals were designated as "immature" if the most advanced oocytes were unyolked or partly yolked without substantial atresia, "ripening mature" if fully yolked but lacking POF or HYD, "resting mature" if a majority of the yolked oocytes were atretic, or "ripe mature" if POFs or HYDs were present. Fish that might in the future have resorbed yolked oocytes without spawning were necessarily classified as mature.

Statistical analyses

We used oocyte volume (OV) to characterize egg size because a volumetric measure was more directly proportional to OW than was a linear measure such as oocyte diameter. OV was calculated as the volume of a sphere, $4/3\ \pi r^3$, where r was one-half of the median diameter of the largest oocytes (Lau and DeMartini, 1994). The sampling distributions of dependent and regressor variables were first examined by using raw and log-transformed data. Log-transformed data were least skewed; logarithms (base 10) were therefore used in all subsequent analyses.

We used analysis of covariance (ANCOVA) to determine if OW was suitable for quantifying maturation state of individual fish after adjusting OW for body size, egg size, or both measures. For each species, the analysis evaluated fish of three ovarian developmental stages (unripe immature, ripening or resting mature, and ripe mature), identified histologically. We were thereby able to evaluate the potentially confounding effects of oocyte development and body size on ovary weight (Erickson et al., 1985b).

We further used two classification techniques (discriminant analysis and logistic regression) to distinguish between mature and immature fish. These two techniques were used because we recognized the general need, in studies such as this, to classify the maturity status of individual fish 1) based on both gross morphometrics and histological criteria and 2) with gross metrics alone, without the added benefit of histological evidence. At a minimum, ovary tissues of some of the fish examined in any study need to be examined histologically as a check on the accuracy of gross classification.

Both logistic regression and discriminant analysis can be used to classify dichotomous states such

as maturity. The latter is often (Efron, 1975), but not always (Prager and Fabrizio, 1990), the more effective technique. However, it is less robust to violations of the assumption of identical covariance matrices. Multivariate normality is also assumed if linear discriminant functions are fitted parametrically (Press and Wilson, 1978), an assumption we avoided in this study (see below).

For combined gross-histological classifications of maturity, we used predictive discriminant analysis (Huberty, 1994) to distinguish between mature (ripe, ripening or resting) and immature fish. Nonparametric discriminant functions were derived by using the uniform-kernel method with Euclidean distances (Huberty, 1994). We used logistic regression (Hosmer and Lemeshow, 1989) to evaluate whether maturity classifications based on histology could be predicted by the relationships among body size, OW, and OV. Logistic regression coefficients were estimated by maximum likelihood methods. Using each technique, we evaluated the full (three-variable) model first, then a two-variable model without OV. Because sample sizes were small for each species, all sample fish of each species were evaluated histologically.

Once all individuals had been assigned to maturity classes based on histological and gross morphometric criteria, we assigned specimens to 2-cm length classes and calculated the percentage mature for each length class using each set of criteria. Percent maturity (0–100%) was then related to length class by using nonlinear regression weighted by the square root of the numbers of fish in each length class. The logistic model,

$$P_x = 100 / \left(1 + e^{(a+bFL)}\right),$$

where P_x = percentage mature in each length class;
a and b = fitted parameters; and
L_{50} = $(-a/b)$, was fitted to the data by using maximum likelihood.

Data were analyzed using STATISTIX (v. 4.1; Analytical Software, 1994: logistic regression) and SAS (v. 6.03; SAS Institute, Inc., 1988: PROC REG, GLM, and DISCRIM).

Results

Body size interrelations

After log-transformation, the influences of body length (FL) and ovary-free body weight (OFBW) on ovary weight (OW) were virtually identical; hence, FL (the easier variable to measure) only is reported in Table 2 and used in all subsequent analyses. OFBW was significantly related to FL for each species (ehu: $\log OFBW = -1.720 + 2.971 \log FL$, $r^2=0.979$, $n=172$, $P<0.001$; kalekale: $\log OFBW = -1.785 + 3.010 \log FL$, $r^2=0.966$, $n=75$, $P<0.001$).

Effect of ovarian stage on relation of ovary weight to body length

The OW-to-body length relation marginally differed with ovarian developmental stage for ehu and kalekale (FL × stage interaction in ANCOVA: $F_{2,175}=3.19$ and $F_{2,74}=2.69$, $P=0.04$ and 0.06, respectively; reject H_0: slopes equal). Thus, ovary weights could not be adjusted by body lengths and subsequently used to distinguish among maturation states for either species. Body length was a poor predictor of ovary weight for both ehu and kalekale ($r^2=0.58$ and 0.60, respectively; Table 2).

Effect of egg size

FL and OV together, however, accounted for 91% (ehu) and 82.5% (kalekale) of the variation in OW (Table 2). Colinearity between FL and OV (or OFBW and OV) was unimportant. For example, FL explained only 12% of the variation in OV for ehu.

Histological evidence of maturity

Most specimens of ehu and kalekale were readily classified as either immature or mature according to histological criteria. Kalekale included fish that were immature, ripening mature, and ripe mature (none were resting mature). Unlike kalekale, a minority of the large (>40 cm FL) ehu were resting mature, with ovaries undergoing substantial atresia. The ovaries of kalekale usually contained HYD oocytes if POFs were present (19 of 21 cases). Ehu included specimens with HYD oocytes (7 cases) or POFs (98 cases), but POFs were not observed if HYDs were present (0 of 7 cases). Ehu and kalekale clearly differed in the co-occurrence of HYD oocytes and POFs (Fisher exact test; $P<0.001$), suggesting that the average spawning intervals of individual females probably differ between these two species.

Statistical classifications of maturity

For both species, maturity classifications based on discriminant analysis of the three gross metrics (body length, ovary weight, and oocyte volume) generally agreed (≈98% correct) with those where histological criteria were used (Table 3). Maturity classes determined by histology also were accurately predicted

Table 2

Multiple regression models describing the interrelations of ovary weight (OW), fork length (FL), and oocyte volume (OV) for two species of eteline lutjanids in Hawaii (ehu, *Etelis carbunculus*; kalekale, *Pristipomoides sieboldii*). Mean square errors (MSE) and standard errors of estimates (SE) are noted, with coefficients and standard errors (SE) of model parameters expressed as base 10 logarithms. All regressions are significant, as are the intercepts (all $P<0.001$).

Species	Model $Y = f(X_1+X_2+X_1X_2)$	R^2	n	MSE	Coefficient b_1	b_2	b_{12}	SE SE_{b1}	SE_{b2}	SE_{b12}	Intercept
Ehu	$OW = f(FL)$	0.579	172	0.102	4.541	—	—	0.297	—	—	−5.839
	$OW = f(FL + OV)$	0.911	172	0.022	3.284	0.457	—	0.146	0.018	—	−5.508
	$OW = f(FL + OV + FL \times OV)$	0.917	172	0.020	1.077	−.501	0.627	0.646	0.274	0.179	−2.149
Kalekale	$OW = f(FL)$	0.596	75	0.111	7.007	—	—	0.676	—	—	−9.579
	$OW = f(FL + OV)$	0.825	75	0.049	3.877	0.376	—	0.551	0.039	—	−6.297
	$OW = f(FL + OV + FL \times OV)$	0.826	75	0.049	4.424	0.583	−.139	2.308	0.849	0.569	−7.108

Table 3

Summary results of discriminant analysis evaluating the relations among fork length (FL), ovary weight (OW), plus oocyte volume (OV), for ehu (*Etelis carbunculus*) and kalekale (*Pristipomoides sieboldii*). Analogous summary results using FL and OW only. Imm = immature; Mat = mature.

Species	No. classified by histology as	No. classified by analysis as: Imm	Mat	Total	% Error
FL, *OW*, plus *OV*					
Ehu	Imm	33	0	33	0.00
	Mat	3	145	148	2.03
	Total	36	145	181	1.66
Kalekale	Imm	15	0	15	0.00
	Mat	1	64	65	1.54
	Total	16	64	80	1.25
FL and *OW*					
Ehu	Imm	33	0	33	0.00
	Mat	12	136	148	8.11
	Total	45	136	181	6.63
Kalekale	Imm	14	1	15	6.67
	Mat	3	62	65	4.62
	Total	17	63	80	5.00

(ehu: 97%, kalekale: 100%) by logistic regression using FL, OW, and OV as regressor variables (Table 4). Misclassification errors increased by 3.75–5% (discriminant analysis; Table 3) or 0–5% (logistic regression; Table 4) if oocyte volume was excluded as a predictor of maturity.

Table 4

Summary statistics for logistic regressions used to classify maturity (immature, mature) of ehu (*Etelis carbunculus*; n=181) and kalekale (*Pristipomoides sieboldii*; n=80). Histological maturity was regressed on log-transformations of three gross metrics (fork length, FL; ovary weight, OW; plus egg volume, OV), and FL and OW only. Intercepts and higher-order terms were tested for each model and species, but are unspecified if insignificant.

Species	Regressor	Coefficient: Estimate	SE	Prob
Three-variable model				
Ehu	*FL*			ns
	OW	−13.10	6.82	0.055
	OV	−2.64	0.76	0.001
	$OW \times OV$	8.03	2.58	0.002
Total df: 178				
Overall percentage error: 2.8%				
Kalekale	FL			ns
	OW	−309.4	125.3	0.014
	OV	−9.55	5.26	0.069
	$OW \times OV$	125.2	47.2	0.008
Total df: 77				
Overall percentage error: 0%				
Two-variable model				
Ehu	*FL*	−6.08	1.46	<0.001
	OW	12.29	2.75	<0.001
Total df: 179				
Overall percentage error: 2.8%				
Kalekale	FL	−1.74	0.61	0.004
	OW	5.64	1.37	<0.001
Total df: 78				
Overall percentage error: 5.0%				

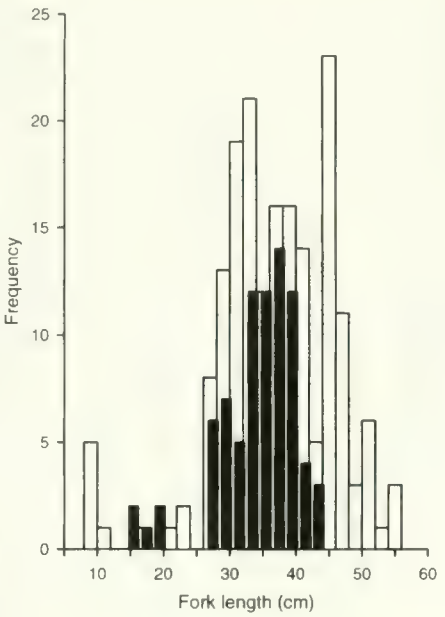

Figure 1

Length-frequency (FL, cm) histograms of ehu, *Etelis carbunculus* (hollow bars, n=181), and kalekale, *Pristipomoides sieboldii* (solid bars, n=80).

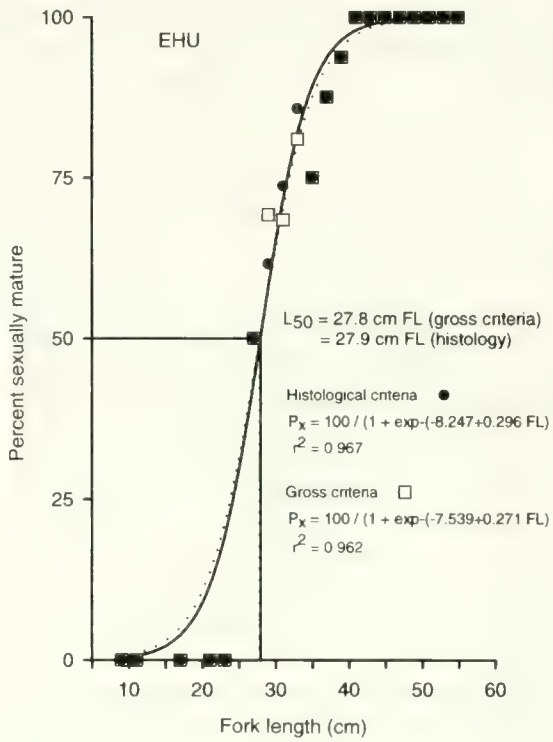

Figure 2

Scatterplots of mean percentage maturity by 2-cm length class, for ehu, *Etelis carbunculus*. Solid circles and solid line represent the observed values and fitted curve based on histological criteria of maturity; hollow squares and dotted line represent the values and curve based on maturity classified by logistic regression on fork length, ovary weight, and oocyte volume. The logistic curves were fitted by nonlinear regression with each class mean weighted by the square root of its count (see Fig. 1).

Size at sexual maturity

For each species, the length-frequency distribution comprised relatively few individuals <30 cm FL (Fig. 1). Hence, our size-at-maturity characterizations might have been affected by the scarcity of immature specimens.

Ehu On average, ehu in Hawaiian waters mature at an estimated 27.9 cm FL (95% CI=25.5–30.3 cm) according to histological criteria or 27.8 (25.5–30.1) cm FL based on logistic regression according to gross criteria (r^2=0.967 and 0.962, respectively; Fig. 2). The precision of these L_{50} estimates is reasonable despite the discontinuous lower tail of the size-frequency distribution. Our L_{50} estimates for ehu provide an adequate objective basis for evaluating gross and histological classifications; however, they should be considered only as preliminary estimates of size at maturity.

Kalekale A body length-maturity pattern also was strongly evident for this species. Whether based on histological evidence or logistic regression with gross metrics, size at maturity was well described by the logistic model (r^2=0.920; Fig. 3). Kalekale in Hawaiian waters mature at 29.0 (95% CI=27.2–30.8) cm FL, according to histological and gross criteria (Fig. 3).

Discussion

Gross metric criteria

For both ehu and kalekale, the proportional weight of ovaries increased allometrically with body length (coefficients of b_1 >> 3; Table 2), which is typical for asynchronous multiple-spawners (Reiss, 1987). Our results further confirm that gonad indices are unsuitable for identifying maturity stages in asynchronous multiple-spawners because the rate at which ovary weight increases with body size differs among fish of different maturation stages (deVlaming et al., 1982; Erickson et al. 1985b). Body size, ovary size,

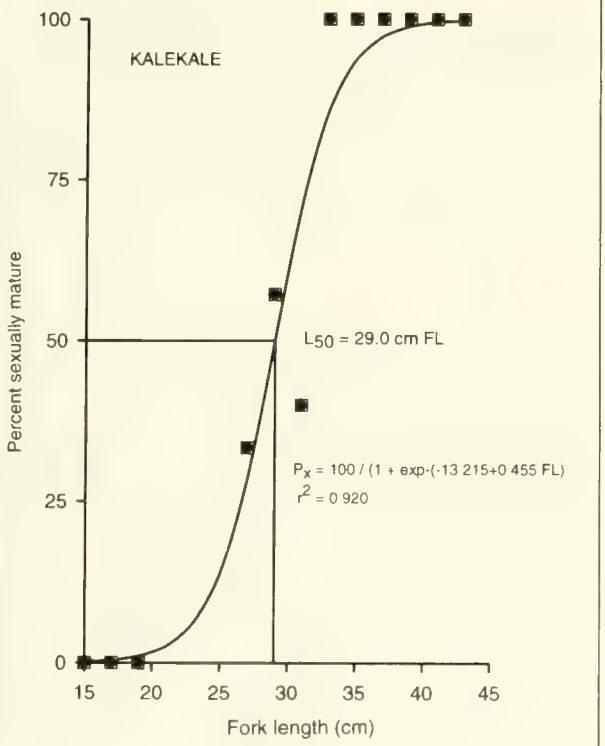

Figure 3

Scatterplots of mean percentage maturity by 2-cm length class, for kalekale, *Pristipomoides sieboldii*. Solid circles inside hollow squares and solid line represent the congruent observed values and fitted curve based on histological criteria of maturity and on maturity classified by logistic regression on fork length, ovary weight, and oocyte volume. The logistic curve was fitted by nonlinear regression with each class mean weighted by the square root of its count (see Fig. 1).

and oocyte size can be used to classify maturity directly by using either discriminant analysis or logistic regression, however. Logistic regression may be more applicable in most studies because of its less stringent assumptions (Press and Wilson, 1978). We recommend using body length for these types of analyses because length data are easier to obtain than weight data.

Relative merits of gross and histological evidence

Histological inspection of stained ovary sections provides the most accurate assessment of sexual maturity, but at the greatest cost. Gross morphometrics can be used to characterize maturity at a greatly reduced cost, but are less accurate predictors. The benefit of a gross morphometric proxy depends on whether the loss in accuracy is outweighed by the cost savings. In our study, assignments of sexual maturity based on discriminant analysis or logistic regression with body length or weight, ovary weight, and oocyte volume were accurate (97–100% correct classification) for ehu and kalekale. Analogous maturity assignments based on only body size and ovary weight (omitting oocyte volume) were less accurate (93–97% correct), indicating a small but real contribution of the egg size variable. Whether the benefit of including an egg size variable merits the cost of its measurement will vary with the particular study. The egg size variable likely had no effect in the logistic regression model for ehu because our specimens included resting mature fish (undergoing oocyte atresia) with small viable oocytes. Two of the three ehu (32.5, 36.2 cm FL) that were misclassified as immature by discriminant analysis with body length, ovary weight, and egg size were resting mature fish. Our ehu data perhaps illustrate discrepancies between gross and histological classifications that might arise when histological criteria for maturity include evidence such as atresia that is unrelated to oocyte mass. Gross criteria likely are most accurate in cases in which samples are collected during peak spawning periods when most fish are actively spawning. Histological criteria may be less than 100% accurate for cases (such as ehu, this study) in which some adolescent fish may resorb yolked oocytes before first spawning (De Veen, 1970; Ramsay and Witthames, 1996). The ability to determine maturity status with reasonable accuracy with only gross metrics in this study nonetheless suggests that such methods warrant further application and evaluation.

Size at sexual maturity

Ehu Our current best estimate of L_{50} for ehu in Hawaiian waters (≈28 cm FL) must be considered preliminary because data for small immature fish are relatively few. Everson (1984), in his pilot evaluation of size at maturity for ehu from Hawaiian waters, also had few small specimens: only 2/185 fish collected during the May–September spawning seasons of 1977–81 were <30 cm FL. Prior to the estimates provided in the present study, those provided by Everson (1984) were the only size-at-maturity estimates available for use in managing ehu in Hawaii (Kobayashi[3]).

Our paucity of specimens <25 cm FL might have reflected hook-size selectivity (Ralston, 1990). How-

[3] Kobayashi, D. R. 1993. Effects of increasing the minimum size limit or imposing fishing closures on three species of Hawaiian deepwater snappers. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Admin. Rep. H-93-01, 18 p.

ever, ehu have relatively large mouths, take baited hooks aggressively (Ralston, 1990), and small-mouthed kalekale were well-represented in our catches. We therefore should have caught small, immature ehu had they been abundant where we fished. Alternatively, juvenile ehu might occupy different bottom depths, as evident for several species of eteline snappers elsewhere (Ralston and Williams, 1988; Parrish, 1989). If so, juvenile ehu inhabit considerably different depths than do larger fish because we fished at depths that were much shallower and deeper than the typical (175–225 m) depths at which adult ehu occur in Hawaiian waters. It is more likely that juvenile ehu occur in different, perhaps lower-relief microhabitats at or near depths at which larger conspecifics are fished in Hawaii (Clarke, 1972; Struhsaker, 1973).

Our estimate of L_{50} for ehu approximates the norm for deepwater lutjanids: 28 cm FL is equivalent to 43% of its reported maximum body length in Hawaiian waters of 65 cm FL (Everson, 1984). On average, deepwater insular snappers mature at about 50% maximum body length, although values can range considerably lower and higher among species (Grimes, 1987).

Researchers must not apply size-at-maturity estimates to other populations of the same species for which somatic condition (Ralston, 1988) or size-specific gonadal allocation might differ, because to do so could result in erroneous estimates of size at maturity. For example, body size at maturity estimated for ehu in this report is applicable only to fish in the Hawaiian archipelago. It is almost certain that body size at sexual maturity differs among Pacific regions, given the great geographic variations in average and maximum body sizes and growth rates of ehu (Smith, 1992; Moffitt, 1993). The L_{50} value for ehu in the South Pacific (Vanuatu), where the species attains maximum body lengths of 120 cm FL, is likely greater than that for ehu in Hawaii. Conversely, our value may be an overestimate in the Marianas, where ehu apparently attain maximum body lengths of less than half those at Vanuatu (Smith and Kostlan, 1991). Improved estimates of L_{50}, based on more data for smaller fish, are needed for ehu in Hawaii. Better age and growth estimates also are needed for ehu in Hawaii and elsewhere because of uncertainties in present size-at-age and growth-rate estimates for the species (Smith and Kostlan, 1991; Kobayashi[3]).

Kalekale We provide the first direct estimates of size at maturity of this species. In age and growth studies of kalekale from the Marianas (Ralston and Williams, 1988) and Hawaiian Islands (Williams and Smith, 1997), deceleration in somatic growth (which should reflect gonadal maturation) occurred at lengths of 25–30 cm FL, consistent with our estimated size at maturity for this species. An L_{50} of 29 cm FL is about 53% of its estimated maximum length in Hawaii (55 cm, as 105% of L_{∞}=52.5 cm FL; Fig. 4 in Williams and Smith, 1997), also approximating the 50% norm for deepwater insular lutjanids (Grimes, 1987).

Conclusions

We believe that gross morphometric measures, such as body size, ovary weight, and egg size, can provide adequate proxies for microscopic histological evidence of sexual maturity in asynchronous multiple-spawners like eteline lutjanids in Hawaii. Applicability may vary among species and may relate to the reproductive dynamics of females, both individually and collectively, within spawning populations. We further suggest that these types of measures can be realistically combined to assess sexual maturity using logistic regression or discriminant analysis for other species of temperate and tropical marine fishes.

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Age and growth of cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico

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Abstract.—We examined 1005 cobia, *Rachycentron canadum*, from recreational catches in the northeastern Gulf of Mexico from 1987 to 1995. Specimens ranged from 325 to 1651 mm fork length (FL); females had a mean FL of 1050 mm (n=730) and were significantly larger than males that had a mean FL of 952 mm (n=275). The overall male to female ratio was 1:2.7. Ages of 565 cobia were estimated from thin-sectioned otoliths (sagittae). Marginal-increment analysis of sagittal otoliths showed a single annual minimum during June. Male cobia (n=170; 525–1330 mm FL) ranged from age 0 to 9, and females (n=395; 493–1651 mm FL) ranged from age 0 to 11. The relationship of observed fork length and age was described by the von Bertalanffy growth equation for males $FL_t = 1171(1-\exp[-0.432(t+1.150)])$ and for females $FL_t = 1555(1-\exp[-0.272(t+1.254)])$. Growth in length for both sexes was relatively fast through age 2, after which growth slowed gradually. Estimates of the von Bertalanffy growth equation parameters L_∞ and K were significantly different for males and females, whereas estimates for t_0 were not significantly different. Sagittal otolith weight was a good predictor of age. The instantaneous rate of total mortality (Z) estimated by catch curve analysis for fully recruited ages 4–8 was 0.75.

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Cobia, *Rachycentron canadum*, are large, migratory, coastal pelagic fish of the monotypic family Rachycentridae and are distributed worldwide in tropical and subtropical seas, except for the eastern Pacific (Briggs, 1960; Shaffer and Nakamura, 1989). In the western Atlantic Ocean, cobia occur from Massachusetts and Bermuda to Argentina (Briggs, 1958) but are most common along the U.S. south Atlantic coast and in the northern Gulf of Mexico (Shaffer and Nakamura, 1989). In the Gulf of Mexico (Gulf), where they range from Key West, Florida, along the entire coast to Campeche, Mexico (Dawson, 1971), *R. canadum* is a highly-prized recreational species and is caught incidentally in several commercial fisheries (Shaffer and Nakamura, 1989). Cobia landings, recreational and commercial combined, from the Gulf and Atlantic averaged one million kilograms (kg) per year during a recent 12-year period (1984–95), of which 87% was recreational catch.[1] The majority of recreational landings of cobia in the United States are from the Gulf (Shaffer and Nakamura, 1989) and averaged 0.5 million kg for years 1984-95.[1] Recreational and commercial cobia regulations enacted in U.S. waters presently consist of a minimum size of 838 mm fork length (33 inches) and daily bag and possession limits of two fish per person.[2]

In the eastern Gulf, cobia typically migrate from their wintering grounds off south Florida into

[1] Gulf of Mexico and South Atlantic Fishery Management Councils. 1996. Report of the mackerel stock assessment panel meeting, April 15–18, 1996, Tampa, FL. Gulf Mex. Fish. Manage. Counc., Tampa, FL, and South Atlan. Fish. Manage. Counc., Charleston, SC.

[2] Gulf of Mexico and South Atlantic Fishery Management Councils. 1990. Amendment No. 5, fishery management plan for the coastal migratory pelagic resources (mackerels); environmental assessment and supplemental regulatory impact review. Gulf Mex. Fish. Manage. Counc., Tampa, FL, and South Atlantic Fish. Manage. Counc., Charleston, SC.

northeastern Gulf waters during early spring. They occur off northwest Florida, Alabama, Mississippi and southeast Louisiana from late-March through October, and return to their wintering grounds in the fall (Franks et al., 1991; Biesiot et al., 1994). Howse et al. (1992) reported that some cobia overwinter in the northern Gulf at depths of 100–125 m.

Information on the life history of cobia from the Gulf and U. S. Atlantic coast is limited. Most studies from the Gulf have addressed the occurrence and distribution of early life stages (Dawson, 1971; Ditty and Shaw, 1992), reproductive biology (Biesiot et al., 1994; Lotz et al., 1996; Thompson et al.[3]), and feeding (Knapp, 1949, 1951; Miles, 1949; Franks et al., 1996; Meyer and Franks, 1996). Hassler and Rainville (1975) collected cobia eggs from the Gulf Stream off North Carolina, successfully hatched most of them, and reared the larvae through juvenile stages. Mitochondrial DNA analyses of cobia from the northeastern Gulf and U.S. Atlantic coast suggest that cobia from those two areas are a unit stock (Hrincevich, 1993). Biesiot et al. (1994) induced spawning in ripe, wild-caught females from the northeastern Gulf, Howse et al. (1975, 1992) described diseased heart tissues and ubiquitous perivenous smooth muscle cords in viscera of cobia from northern Gulf waters, and Franks (1995) reported on an anomalous specimen collected off Mississippi. Only a limited amount of information is available on the age and growth of cobia from the Gulf (Thompson et al.[3]; Franks and McBee[4]) or the U.S. Atlantic coast (Joseph et al., 1964; Richards 1967, 1977; Smith, 1995). The objectives of our study were to evaluate sectioned sagittal otoliths for ageing cobia from the northeastern Gulf, construct age-length keys, derive theoretical growth parameters, and obtain length-weight relationships.

Materials and methods

We sampled cobia caught by recreational hook-and-line gear in the northeastern Gulf during 1987–95. Cobia were sampled at the dock and at fishing tournaments. Fish were caught in an area located north of lat. 29°N and between long. 85°20'W and long. 89'W (Fig. 1) in waters that ranged from 2 to 200 m deep. Additional specimens from northwest Florida were provided by the National Marine Fisheries Service (NMFS), and marine enforcement personnel with the NMFS and the Mississippi Department of Marine Resources provided confiscated undersized specimens. Owing to the migratory nature of cobia, abundance varied seasonally. Most fish that we examined

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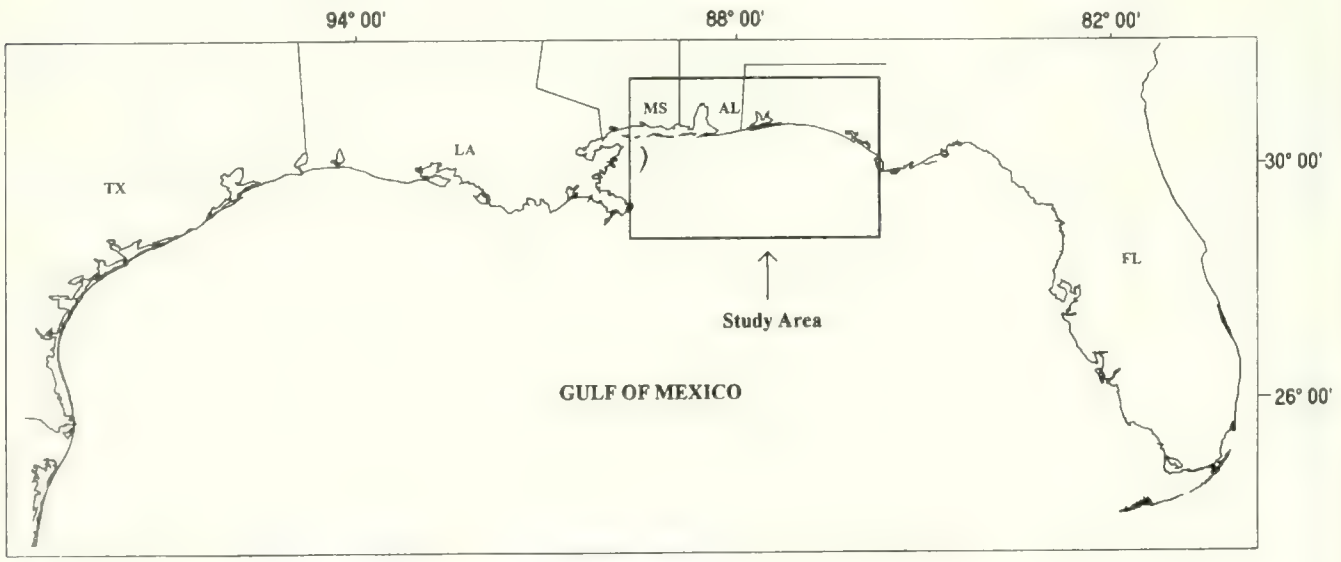

Figure 1

Map of the Gulf of Mexico showing the northeastern Gulf study area where cobia, *Rachycentron canadum*, were caught by hook-and-line gear, 1987–95.

were collected from April through July (n=787); peak samples were taken in May (n=349). Fewer fish were collected in August (n=49) and September through November (n=157). No samples were collected in December, and only 12 samples were collected from January through March.

For most fish, the date and location of catch were recorded along with fork length (FL, mm), total length (TL, mm), and total weight (TW, nearest 0.1 pound converted to kilograms), although some fish had been gutted. All lengths reported are FL. The sex of most fish was also recorded, including that of several young-of-the-year (YOY). Sex-specific length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data, and the slopes and elevations of the regressions were compared by using analysis of covariance (Snedecor and Cochran, 1967). Relationships of fork length to total length were calculated by using the generalized linear regression model: $FL=a+bTL$.

Sagittal otoliths were removed from most specimens, then cleaned with distilled water, air dried, and stored dry in labeled vials. Cobia sagittae are small and fragile. They are elongate, laterally compressed structures, with a rounded posterior, a pointed rostrum, and a smaller, pointed antirostrum (Fig. 2). The distal surface is concave, and a wide, curved sulcus traverses the proximal surface longitudinally. Initially, we randomly selected ten sagittal otolith pairs (fish FL=700–1613 mm) to determine the number of opaque bands in each. Paired counts of opaque bands agreed in all cases. Therefore, the left sagittal otolith was used for age estimation unless missing, broken, or illegible, in which case the right sagitta, if available, was substituted for age analysis. Whole left sagittae were weighed on a microbalance to the nearest milligram to evaluate otolith weight as a predictor of age. Sex-specific linear regressions were fitted to otolith weight and age data and were compared by using analysis of covariance (Snedecor and Cochran, 1967); degree of significance set at $\alpha = 0.05$. Sagittae were embedded in Spurr (Secor et al., 1992) and sectioned through the core along a transverse, dorsoventral plane with a Buehler Isomet low-speed saw containing a diamond wafering blade. Two or three thin-sections (0.3 mm) were mounted on a microscope slide with CrystalBond 509 adhesive, sanded with wet 600- and 1500-grade sandpaper, polished on a felt wheel with 0.3 µm alumina micropolish, then examined under a binocular dissecting microscope at 20–40× magnification with transmitted light.

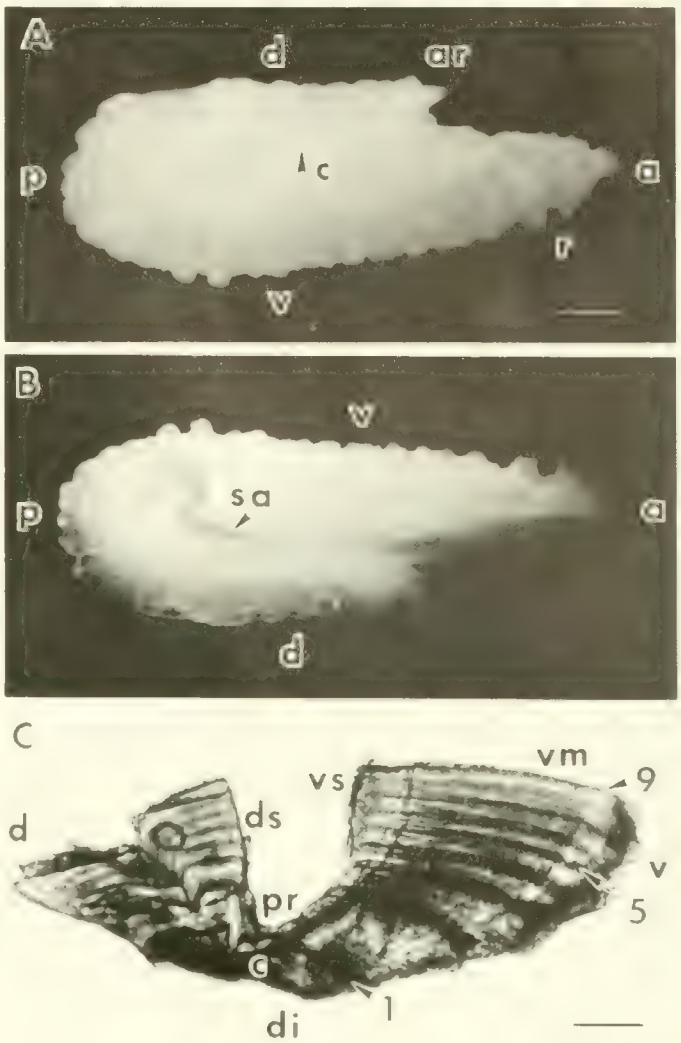

Figure 2

Whole (**A** and **B**) and sectioned (**C**) sagittal otolith from an age 9 (1621 mm FL) female cobia, *Rachycentron canadum*. The otolith's distal (A) and proximal (B) surfaces were viewed with reflected light, and C was viewed with transmitted light. Labels for A and B: a = anterior; p = posterior; d = dorsal; v = ventral; c = core; r = rostrum; ar = antirostrum; sa = sulcus. Labels for C: d = dorsal; v = ventral; di = distal; pr = proximal; c = core; ds = dorsal sulcal ridge; vs = ventral sulcal ridge; vm = ventral margin. Numbers indicate selected annuli. Scale bars = 1.00 mm for A and B; 0.50 mm for C.

Three experienced readers independently counted opaque bands from the core to the outer otolith margin. Opaque bands were most distinct and easily counted in the midportion of the ventral lobe of a section, and our analyses were made in that region (Fig. 2). Opaque bands were often obscured at the

core or confluence with the sulcus acousticus. Opaque bands were initially counted as annuli until they could be properly validated. Annuli were counted without reference to fish length or date of capture. Where counts disagreed, otolith sections were re-examined jointly, and most disagreements were resolved. Unresolved counts and illegible otoliths were excluded from the analysis. Structural aberrations in otoliths judged unsuitable for age estimation included poorly defined annuli, unusual calcification, and erosion of the ventral lobe. Terminology for otolith readings followed definitions of Wilson et al. (1987).

We determined the periodicity of annulus formation and validated our ageing technique by marginal-increment analysis. As recommended by Beamish and MacFarlane (1983), all age classes were included in the analysis. Measurements for marginal-increment analysis were made in the ventral lobe of the magnified (30×) section by using a digital imaging system. Distances were measured ventrally from the sulcus along an axis passing through the center of the lobe and extending from the otolith's core to the outer margin of the section. The distance from the proximal edge of the ultimate annulus to the otolith's margin (marginal increment) was expressed as a percentage of the distance between the proximal edge of the last two annuli formed on the otolith. This procedure was adapted for age 1 fish by expressing the marginal increment as a percentage of the distance from the edge of the first annulus to a hypothetical second annulus (Crabtree et al., 1996). Mean percent marginal increments were plotted for all age groups and collection years combined by month of capture.

The von Bertalanffy (1957) theoretical growth equation, $FL_t = L_\infty(1-\exp[-K(t-t_0)])$, was fitted to observed age-length data with the nonlinear regression procedure of Statgraphics (1994). Likelihood-ratio tests (Kimura, 1980; Cerrato, 1990) and approximate randomization tests (Helser, 1996) were used to compare growth parameter estimates for males and females. Sexed YOY were included in the growth models.

Observed ages at lengths for all years combined were used to derive an age-length key for each sex (Ricker, 1975). Aged fish (n=565) were assigned to 50-mm length intervals, and age distribution (as percent) was then calculated for each size interval. Age-length keys were used to convert length frequencies to age frequencies by assigning ages to unaged fish ≥838 mm FL from which a catch curve (Ricker, 1975) was constructed for 1987–92. We estimated instantaneous total mortality (Z) by catch curve analysis (Beverton and Holt, 1957; Everhart and Youngs, 1981) based on fully recruited fish.

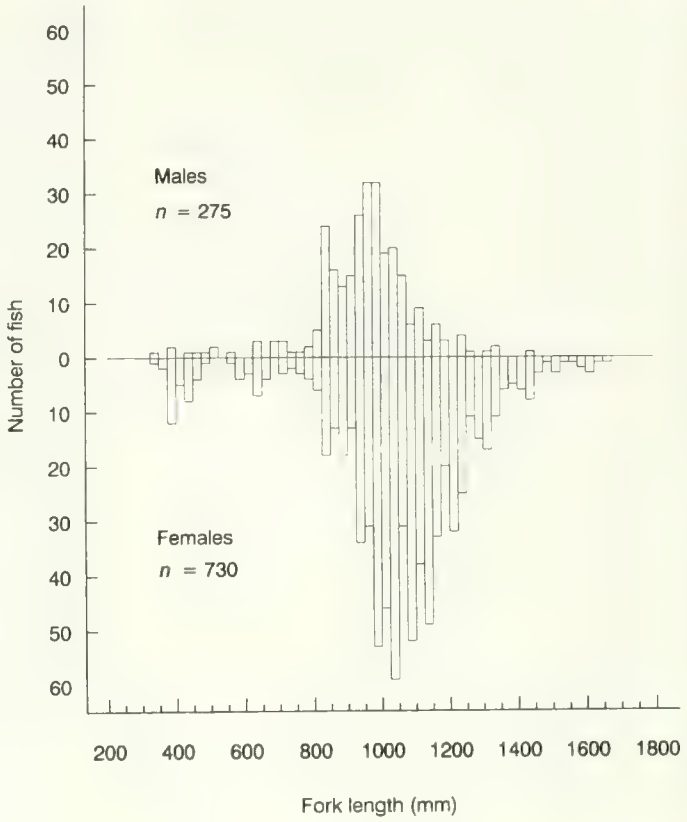

Figure 3

Length-frequency distributions (25 mm increments) for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico collected during 1987–95.

Results

We examined 1005 cobia that ranged from 335 to 1651 mm FL, 33 of which were YOY (age 0) and ranged from 335 to 510 mm FL. External sexual dimorphism was not evident in *R. canadum*. Males (n=275) ranged from 345 to 1450 mm FL (mean=952 mm) and from 0.3–29.0 kg (mean=10.5 kg); females (n=730) ranged from 335 to 1651 mm FL (mean=1050 mm) and from 0.3 to 62.2 kg (mean=16.6 kg). The length-frequency distributions of males and females (Fig. 3) were significantly different (Kolmogorov-Smirnov two-sample test, d=0.432, P<0.05). Females

were significantly larger than males (Mann-Whitney U-test, $P<0.001$), and 85% of fish ≥1000 mm were female. The sex ratio of 1:2.7 was significantly different from 1:1 ($\chi^2=205.8$, df=1, $P<0.0001$).

Neither slopes (ANCOVA, df=914; $F=2.156$, $P=0.142$) nor elevations (ANCOVA, df=914, $F=2.334$, $P=0.127$) of the length-weight regressions by sex were found to be significantly different; therefore, data were pooled and one relationship established (Table 1; Fig. 4). Weight was approximately a cubic function of length, implying nearly isometric growth. The relationships between FL and TL are presented in Table 1.

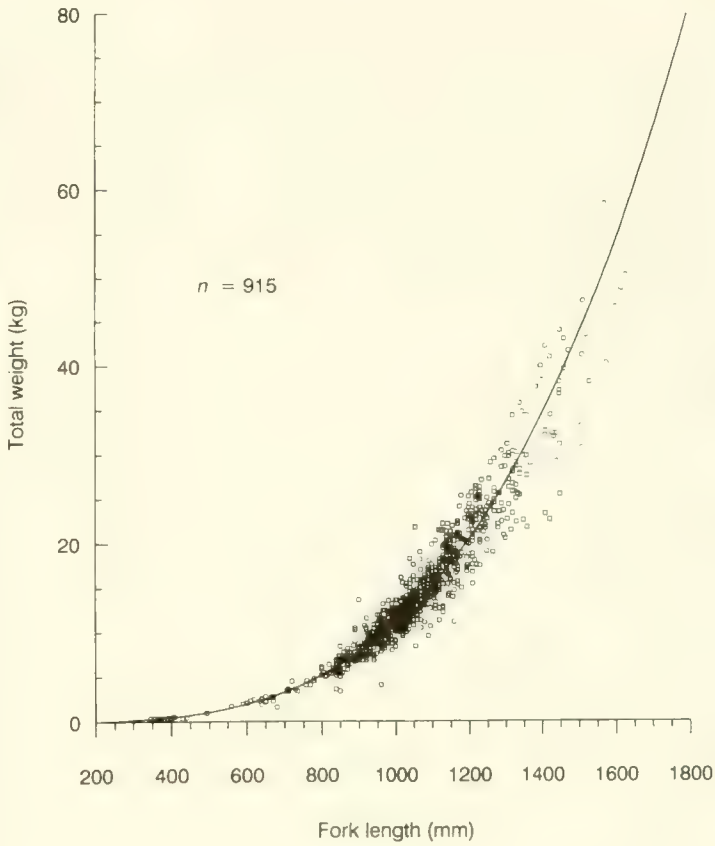

Figure 4

Length-weight relationship for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico.

When viewed with transmitted light, thin-sectioned sagittae revealed a pattern of distinct, alternating narrow opaque and wide translucent bands (Fig 2). The distance between the first two opaque bands distally from the core typically was wider than the distance between subsequent opaque bands. Mean marginal increment analysis (Fig. 5) demonstrated that April through August was the time of annulus formation and suggested that opaque bands form once each year. All otoliths exhibited a zone of translucent material beyond the last annulus from September through February. Mean increment was minimal during June and increased to a maximum in February (no samples were collected during December). The sample size was too small to plot marginal increments for each year and age-group separately; however, a visual examination of the data indicated that marginal increments for individual years 1987–90 and age-classes 2–5 were similar, with a consistent seasonal minimum during summer. Timing of annulus formation was similar for each sex.

Of the 645 left sagittae processed for age estimates, 187 (29%) were judged illegible. Right sagittae from 168 of the latter group were available and processed, and 76% (128/168) were readable. Readers agreed on ages for 96% (565/586) of usable otoliths, 170 males (range 345–1330 mm FL) and 395 females (range 335–1651 mm FL). Only 21 (4%) of the usable otoliths were rejected because of disagreements among readings, owing primarily to disparities over the presence of an annulus adjacent to the core or at the otolith's margin. Of the sagittae found acceptable for age estimations, 33 were from YOY (335–510 mm) and 42 were from age 1 fish (493–910 mm). Ten age 1 fish were 838 mm (minimum legal size) or larger. Most (n=463, 82%) of the 565 fish that we aged were estimated to be ages 2–5 (27% age 2; 29% age 3; 17% age 4; and 9% age 5). Age 6 fish and older were conspicuously uncommon. There was a significant difference between the age-frequency distributions of males and females (Kolmogorov-Smirnov two-sample test, dn=0.308, $P<0.05$). An age 11 female (1568 mm) and age 9 males (n=2, 1240 and 1260 mm) were the oldest cobia sampled (Table 2). Twenty five females (1170–1651 mm) were age 6 or older, but only six males (1035–1330 mm) were older than age 5 (Table 2).

Growth in length for both sexes was relatively fast through age 2, after which growth slowed gradually (Fig. 6). We found a wide range of lengths within most age groups for both sexes (Tables 3 and 4). For example, age 4 males and females ranged from 850 to 1250 mm and from 900 to 1250 mm, respectively. We also found a wide range of ages within some of the length groups. For example, the 1000 mm and 1200 mm groups of males ranged from ages 2 to 7 and from

Table 1

Length-length, length-weight, and otolith weight-age regressions for cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico. FL = fork length (mm), TL = total length (mm), WT = total weight (kg), OTWT = otolith weight (g), and AGE = age in years. Sample fork length range for length-length regressions and length-weight regressions was 345–1651 mm. Age range for the otolith weight-age regression was 1–9 for males and 1–11 for females. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a	b	r^2
FL	TL	930	9.9494 (3.5691)	0.8916 (0.0032)	0.989
TL	FL	930	1.6661 (3.9964)	1.1088 (0.0040)	0.989
$\log_{10}$WT	$\log_{10}$FL	915	−9.2445 (0.6474)	3.4287 (0.0215)	0.965
OTWT (males)	AGE	126	0.0081 (0.0012)	0.0072 (0.0003)	0.775
OTWT (females)	AGE	259	0.0006 (0.0010)	0.0110 (0.0003)	0.836

Table 2

Average observed and predicted fork lengths (mm) for male and female cobia, *Rachycentron canadum*. Numbers in parentheses are standard error and sample size.

	Males		Females	
Age (yr)	Average observed	Predicted	Average observed	Predicted
0	439 (29.6;5)		409 (6.0;28)	
1	705 (26.0;14)	709	720 (21.6;28)	713
2	885 (8.5;47)	871	956 (7.9;103)	914
3	971 (9.9;47)	976	1056 (7.2;116)	1066
4	1034 (14.2;35)	1044	1140 (10.4;64)	1183
5	1070 (16.6;16)	1089	1248 (17.6;31)	1271
6	1140 (1)	1118	1346 (37.9;7)	1339
7	1198 (86.5;3)	1136	1385 (44.0;5)	1391
8		1148	1553 (27.4;8)	1430
9	1250 (10.0;2)	1156	1507 (69.9;3)	1460
10			1613 (1)	1482
11			1568 (1)	1500

Table 3

Age-length key. Fork length (mm) composition, in percent, of male cobia by age group

Length group (50 mm)	Age in years										Number of fish
	0	1	2	3	4	5	6	7	8	9	
300	100.0										1
350											
400	100.0										1
450	100.0										2
500	50.0	50.0									2
550		100.0									1
600		100.0									2
650		100.0									2
700		100.0									4
750		100.0									1
800		11.1	83.3	5.6							18
850		4.8	66.7	19.0	9.5						21
900			40.9	50.0	9.1						22
950			20.6	50.0	29.4						34
1000			9.1	27.3	22.7	36.4		4.5			22
1050				35.3	41.2	23.5					17
1100					66.7	22.2	11.1				9
1150				50.0	50.0						4
1200					20.0	40.0		20.0		20.0	5
1250										100.0	1
1300								100.0			1
Total											170

ages 4 to 9, respectively (Table 3), whereas the 1350 mm group of females ranged from ages 5 to 9 (Table 4).

The results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=175.06, df=1, P<0.0001) (Table 5), a finding substantiated by approximate randomization testing of the growth models (P<0.0001). Likelihood-ratio tests showed that estimates of L_∞(χ^2=24.60, df=1, P<0.0001) and K (χ^2=7.02, df=1, P=0.008) were signifantly different between sexes, however, t_0 was not significantly different (χ^2=–0.11, df=1, P=0.752). Growth parameters indicated that females achieved a greater theoretical asymptotic length and grew at a faster rate than males. Predicted lengths-at-age derived by the von Bertalanffy equations agreed with observed lengths, except for age 9 males (n=2) and age 8 and 10 females (n=12) (Table 2), where observed lengths were considerably larger than those predicted. Average observed lengths-at-age for females were greater than those of males for age 1 and older (Table 2), and predicted lengths of females were greater than those of males for all ages.

Otolith weight was significantly related to age (Fig. 7), and the slopes of the otolith weight-age regressions for males and females (Table 1) were significantly different (ANCOVA , df=385, F=34.13, P<0.0001).

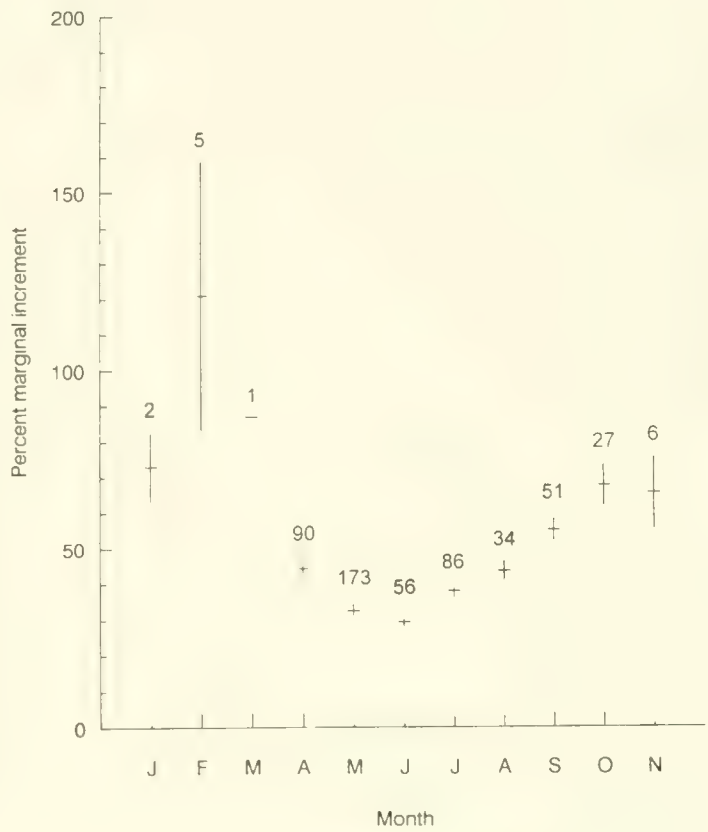

Figure 5

Monthly mean percent marginal increment for cobia, *Rachycentron canadum*. Vertical lines represent ±1 SE. Numbers above vertical lines represent sample size.

Age-length keys were constructed to estimate the age structure of legal-sized cobia (≥838 mm FL) caught from 1987 to 92 (Fig. 8) which we believe was representative of the northeastern Gulf recreational fishery. Most (84%) of those fish were age 2–4, whereas age 3 represented 37% of the catch. Age at full recruitment to the fishery was age 4 (modal age plus one). Ages 1–3 represented 66% of the fishery, age 4 represented 19%, and ages 5–11 only 15%. The instantaneous rate of total mortality (Z) estimated by our catch curve analysis for ages 4–8 was 0.75 (Fig. 9).

Discussion

Despite acquiring many of our cobia samples at fishing tournaments, we believe our overall collections reflect the recreational hook-and-line fishery for cobia in the northeastern Gulf during the late 1980s and early 1990s. Although anglers typically enter large fish in tournaments, substantial numbers of small fish were also entered during the competitions, particularly if aggregate weight awards were presented during multiday competitions. We frequently sampled anglers' entire catch which included small fish not entered in competition. Nontournament fish were also examined at docks and marinas, and these specimens ranged from less than minimum legal size to some of the largest fish that we encountered.

Although the length-weight relationships between the sexes did not differ significantly, females were typically larger than males. Thompson et al.[3] reported similar results for cobia taken off western Louisiana. In our study, females predominated (2.7:1 overall sex ratio) during all study years. Females were dominant in all age groups, and the magnitude of that dominance varied with increasing age. During a five-year study (1987–91) of cobia from western Louisiana waters (west of the Mississippi River delta), Thompson et al.[3] reported an overall sex ratio of 2.1:1 that was skewed towards males (464,

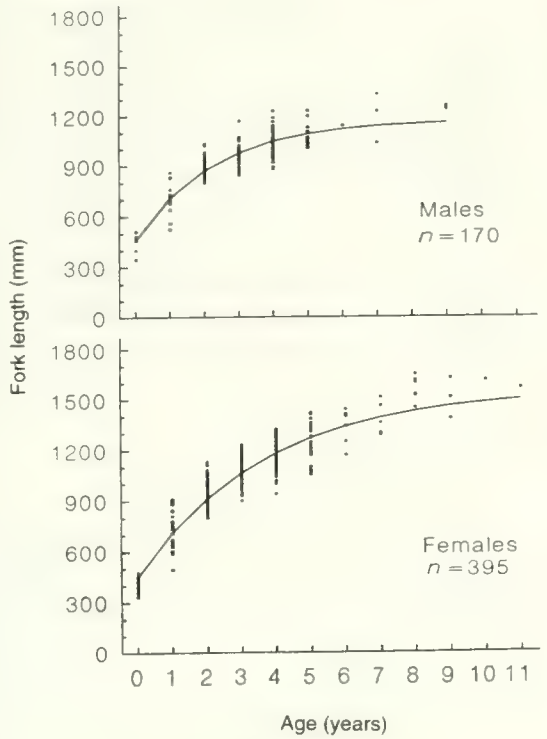

Figure 6

Observed and predicted lengths from the von Bertalanffy growth model for male and female cobia, *Rachycentron canadum*.

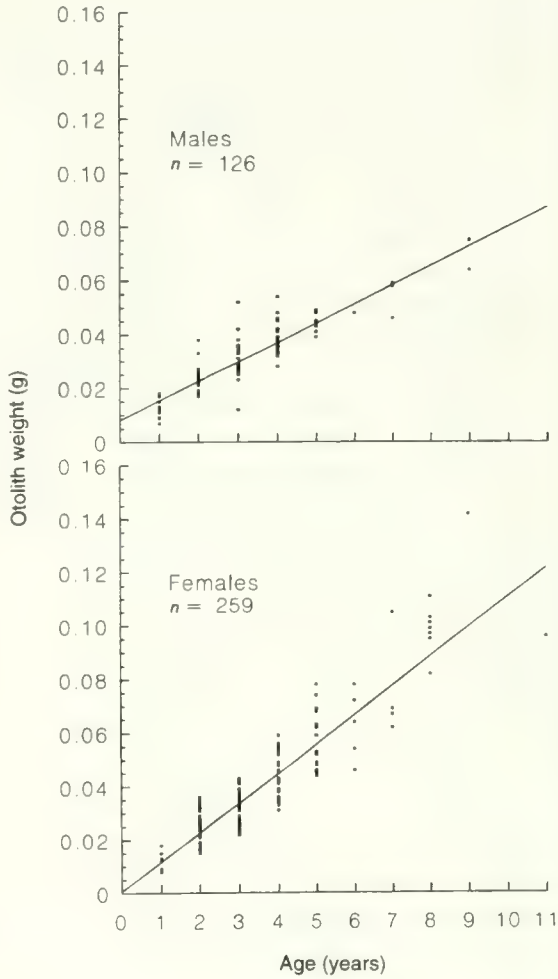

Figure 7

Sagittal weight-age relationship for male and female cobia, *Rachycentron canadum*.

males; 218 females) for each year. Because our study and that by Thompson et al.[3] were conducted concurrently, we are unable to explain this discrepancy, except to suggest differential segregation or a higher mortality for males east of the delta.

Sagittal otoliths were determined to be valid ageing structures for *R. canadum*, and alternating opaque and translucent bands were most conspicuous in the ventral lobe of otolith thin-sections. Annuli were not uniformly visible in thin-sections for some fish and were occasionally obscured along the ventral sulcal ridge, particularly for fish age 5 and older. Marginal-increment analysis indicated that annuli formed once per year during April–August. Therefore, age in years for cobia was presumed equal to the number of opaque bands observed in sectioned sagittae, findings that agree with those of Thompson et al.[3] off Louisiana and Smith (1995) off North Carolina. Because cobia are infrequently caught in northeastern Gulf waters during the winter, the scarcity of otolith samples from November through March precluded us from making an unequivocal assertion on the annual nature of opaque band formation. However, thin-sectioned sagittae from seven cobia caught in the Florida Keys during January 1991 and sampled dockside by us showed a substantial zone of translucent material extending from the distal edge of the last opaque band to the otolith margin. This finding suggests that winter annulus formation does not occur in the otoliths of cobia from south Florida waters (cobia that may migrate into northern Gulf waters in spring).

Although the timing of annulus formation coincides with the cobia's spawning season in the northern Gulf (Biesiot et al., 1994; Lotz et al., 1996), annulus deposition may be more related to cobia migration into the northern Gulf in spring. We found that sagittae of several sexually mature cobia sampled in April (early part of the spawning season) already showed opaque bands, as did sexually immature fish in spring. The relationship of annulus formation to

Table 4

Age-length key. Fork length (mm) composition, in percent, of female cobia by age group

Length group (50 mm)	Age in years												Number of fish
	0	1	2	3	4	5	6	7	8	9	10	11	
300	100.0												1
350	100.0												8
400	100.0												17
450	66.7	33.3											3
500													
550		100.0											1
600		100.0											7
650		100.0											5
700		100.0											3
750		100.0											3
800		25.0	75.0										12
850		19.0	81.0										21
900		3.3	66.7	26.7	3.3								30
950			52.2	47.8									46
1000			40.0	47.3	12.7								55
1050			12.2	53.1	28.6	6.1							49
1100			13.2	39.5	44.7	2.6							38
1150				46.4	28.6	21.4	3.6						28
1200				28.6	42.8	28.6							21
1250					40.0	40.0	10.0	10.0					10
1300					33.4	50.0	8.3	8.3					12
1350						60.0		20.0		20.0			5
1400						28.6	57.1		14.3				7
1450								50.0	50.0				2
1500								25.0	50.0	25.0			4
1550												100.0	1
1600									60.0	20.0	20.0		5
1650									100.0				1
Total													395

Table 5

Parameter estimates for the von Bertalanffy growth model for cobia, *Rachycentron canadum*, from U.S. waters. Values shown in parentheses are standard errors. — = not reported by author(s).

Area	Sex	n	L_∞	K	t_0	r^2	Structure	Authors
Virginia[1]	M	—	121	0.28	–0.06	—	scales	Richards, 1967
	F	—	164	0.23	–0.08			
North Carolina[1]	M	116	105	0.37	–1.08	—	otoliths	Smith, 1995
			(1.85)	(0.04)	(0.29)			
	F	92	135	0.24	–1.53			
			(3.82)	(0.03)	(0.39)			
Western Louisiana[2]	M	—	1,132	0.49	–0.49	—	otoliths	Thompson et al.[3]
	F	—	1,294	0.56	0.11			
Northeastern Gulf of Mexico[2]	M	170	1,170.7	0.432	–1.150	0.78	otoliths	This study
			(28.08)	(0.046)	(0.173)			
	F	395	1,555.0	0.272	–1.254	0.87		
			(35.14)	(0.017)	(0.092)			

[1] L_∞ estimates reported in centimeters.
[2] L_∞ estimates reported in millimeters.
[3] See Footnote 3 in text for this source.

migration has been suggested for swordfish (Berkeley and Houde, 1983; Tserpes and Tsimenides, 1995) and Atlantic bluefin tuna (Compean-Jimenez and Bard, 1983). Other authors (Nelson and Manooch, 1982; Sturm et al., 1989; Beckman et al., 1990; Ferreira and Russ, 1994) also suggested that reproduction may not be the sole determining factor and commented on the physiological nature of annulus formation and the importance of environmental factors.

Longevity of male and female cobia differed considerably. Males older than age 7 were rare, and maximum age was 9. Females older than age 8 were rare, and maximum age was 11. Maximum ages of cobia from Louisiana (age 10, Thompson et al.[3]) and Virginia (age 10, Richards, 1967) were similar to our observations. However, Smith (1995) reported a maximum age of 14 for males and age 13 for females for cobia from North Carolina. We also found, as did Richards (1967) and Smith (1995), that mean observed lengths at age for females were larger than those for males for all age classes, except age 0 fish.

Considerable variation in size was observed within most age groups, including YOY, for both males and females, which, according to Goodwin and Johnson (1986), is not unusual for warm-water fishes. The variation in size makes it difficult to estimate precisely the age of cobia from length alone. For example, our largest cobia weighed 62.2 kg, which was slightly greater than the all-tackle world record weight for cobia (61.5 kg) reported by the International Game Fish Association (1997). At a fork length of 1610 mm and at age 8, this specimen was neither the longest fish in our sample nor the oldest. A prolonged spawning season and multiple spawnings characteristic of cobia (Lotz et al., 1996) probably account for the wide variation in size of YOY cobia and other age groups as well. Annual growth was most rapid through age 2 for both sexes, then gradually decreased thereafter, particularly for females.

Otolith weight was a good predictor of age, accounted for 78% and 84% of the variability in age of male and female cobia, respectively, and explained as much variation in age as fork length in the von Bertalanffy model for each sex.

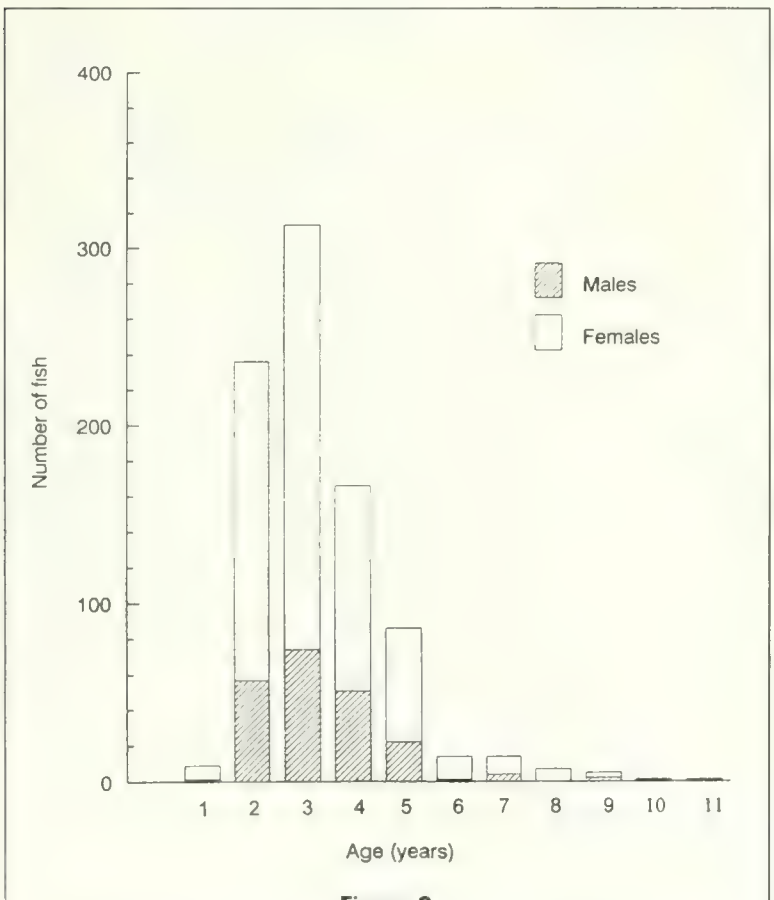

Figure 8

Age structure of cobia, *Rachycentron canadum*, ≥838 mm FL (regulation minimum size) in the northeastern Gulf of Mexico recreational hook-and-line fishery, 1987–92. n=992

Our estimates of growth parameters are the only estimates available for *R. canadum* in the northeastern Gulf. We found that the von Bertalanffy theoretical growth models for males and females were significantly different, as did Thompson et al.[3] Lengths predicted from the theoretical growth curves agreed with the average observed lengths. Theoretical asymptotic lengths seemed realistic, even though few fish >1200 mm were sampled. Theoretical growth coefficients (L_∞ and t_0) reported by Thompson et al.[3] for cobia from Louisiana were smaller than our estimates (Table 5), although their estimates of K were larger, particularly for females. Asymptotic lengths for males and females taken off Virginia (Richards, 1977) were considerably larger than L_∞ values reported by Smith (1995) for cobia from North Carolina, values reported by Thompson et al.[3] for cobia from Louisiana and our study (Table 5), although our asymptotic length for males was similar to that in Richards' (1967) study. The differences in estimates of growth coefficients for cobia throughout their range in U.S. waters may be due to methodological differences, e.g. sectioned otoliths (this study) versus scales (Richards, 1967), or differences in geographical coverage. Nevertheless, we believe our growth parameter estimates are appropriate for

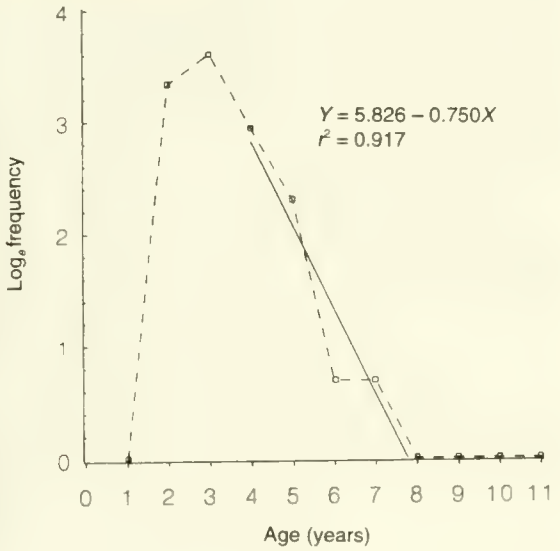

Figure 9

Length-converted catch curve for cobia taken in the northeastern Gulf of Mexico recreational fishery. The solid line described by the equation ($Y=a+bX$) indicates the age range used in regression estimates of instantaneous total mortality (Z). Z is equal to the absolute value of the slope (b) of the regression line.

use in assessment studies of cobia from the northeastern Gulf.

Cobia were fully recruited to the recreational fishery in the northeastern Gulf at age 4. Catch curve analysis predicted a Z of 0.75. A fairly broad age structure and a low value for Z suggest that the northeastern Gulf population of cobia is reasonably healthy. We believe our estimate of Z is reliable, although several authors (Rounsefell and Everhart, 1953; Johnson, et al., 1983; and Manooch et al., 1987) caution against using catch curves to predict mortality for migratory pelagic species because, in part, such predictions are subject to a variety of assumptions, including a constant recruitment and mortality for each year and year class comprising a pooled data set. The popularity of cobia warrants continued monitoring of population age structure and growth parameters of this valuable gamefish in the northern Gulf.

Acknowledgments

We are indebted to the anglers who allowed us to sample their catch of cobia. We thank Barbara Palko, formerly of the National Marine Fisheries Service (NMFS), Panama City (Florida) Laboratory, for making numerous specimens available to us. We express our appreciation to Thomas McIlwain of the NMFS and Richard Leard of the Gulf of Mexico Fishery Management Council for their encouragement and advocacy of our work, particularly in the initial stages of the study. Many thanks to our colleagues in the Marine Fisheries Division of the Mississippi Department of Marine Resources. Chuck Wilson, Bruce Thompson, and Louise Stanley of Louisiana State University, Coastal Fisheries Institute, provided valuable advice and great inspiration. We express our sincere gratitude to Mike Allen and Dyan Wilson for their diligence at the otolith saw and their assistance in reading otoliths. We acknowledge the many contributions of T. J. Becker, the archetypal tournament sampler. We thank Robin Overstreet for photographing the otoliths shown in this manuscript and for sharing with us his interest in the biology of cobia over many years. Many other individuals participated in portions of this study including the following Gulf Coast Research Laboratory personnel: Don Barnes, Lisa Engel, Dale Fremin, Nikola Garber, Nate Jordan, David Lee, Jeffery Lotz, Terry McBee, Casey Nicholson, Steve Vanderkooy, and Mike Zuber. We also offer thanks to Michael Murphy and Roy Crabtree of the Florida Marine Research Institute and to James Duffey of the Alabama Department of Conservation and Natural Resources for their valued advice and assistance on statistical treatment of the data. We recognize colleagues Patricia Biesiot of the University of Southern Mississippi, and Joe Smith and John Merriner of the NMFS Beaufort (North Carolina) Laboratory who share with us a deep appreciation for this great fish. We thank three anonymous reviewers and the scientific editor for their extremely helpful comments and suggestions. This work was supported in part by funding from Federal Aid in Sport Fish Restoration, Department of the Interior, U. S. Fish and Wildlife Service, Atlanta, GA, Project No. F-91, and the Mississippi Department of Marine Resources, Biloxi, Mississippi.

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Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*

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Abstract.—We examined scale samples from historical collections of postsmolts from the Gulf of St. Lawrence, Canada, with the aim of understanding the role of estuarine and coastal habitats as a juvenile nursery for Atlantic salmon. Circuli spacing patterns were extracted from the scales of 580 postsmolts collected in the Gulf during three seasons, 1982–84. Poststratification of the samples by collection date within year suggests that in some years postsmolts remain in the Gulf throughout the entire summer growth season, whereas in other years only slower growing fish remain in these areas. Growth patterns for Gulf of St. Lawrence postsmolts were compared with patterns for returns from three salmon stocks from the southern end of the range in North America. These data suggest that in some years postsmolt growth in the Gulf is as robust as that observed for both the one seawinter (1SW) and two seawinter (2SW) returns to southern rivers. Postsmolts are believed to use oceanic nursery areas generally; thus, comparable growth between the two stock groups suggests that the Gulf may serve as an important part of the postsmolt nursery range in some years. The concept of the postsmolt nursery as a continuum between neritic and oceanic areas is essential to evaluating ocean climate and productivity effects on salmonid recruitment.

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Anadromous salmonids, such as Atlantic salmon, *Salmo salar*, use freshwater stream habitats as nursery areas for their early life history stages (Thorpe, 1994). Freshwater residency provides refuge from potential predators and relatively stable survival conditions for eggs and juveniles (Chaput et al., 1998). Thus, the recruitment of smolts during the freshwater phase is characterized by relatively low annual variability, most of which is attributed to the size of spawning escapements (Chadwick, 1987). As a consequence, the relationships between spawning stock abundance and recruits migrating from freshwater take on predictable forms (Chadwick, 1985; Elliott, 1993). The relationships between generations of spawners, however, are not as clear owing to highly variable rates of marine survival.

The first year at sea, or the postsmolt year, for Atlantic salmon is poorly understood. The transition to the marine environment is in itself a survival challenge associated with specific estuarine habitats (Levings, 1994). After postsmolts make the transition, they are believed to disperse widely in ocean surface waters. This belief stems from the facts that they are rarely caught in nearshore fishing gears and have proven difficult to capture in directed surveys. The exception has been in the Baltic area, where the spatial confines of the Baltic Sea and postsmolt recoveries in commercial fisheries have combined to produce a relative wealth of information on the distribution and survival of postsmolts in that region (Larsson, 1985; Eriksson 1994; Kuikka and Salminen 1994). The equivalent information does not exist for North Atlantic postsmolts; thus, it is critical to learn more about the basic biology of postsmolts so that informed interpretations of the patterns in salmonid population dynamics can be made.

Recoveries of North American versus European postsmolts suggest that habitat use and ecological roles may differ for the early marine stages of the two stock complexes. Recent captures of postsmolts in the Northeast Atlantic show that they are distributed over

a large oceanic region by their first summer at sea (Holm et al., 1996; Shelton et al., 1997). These distribution patterns suggest that postsmolts migrate to the northwest and may be less likely to use inshore neritic habitats. However, in the Northwest Atlantic, the few recovery data available for postsmolts suggest differing views of which habitats represent the nursery area for postsmolts. Salmon postsmolts have been reported to use estuarine waters; therefore it is possible that they possess specific behaviors to orient themselves to inshore areas during their first year at sea (Robitaille et al., 1986; Dutil and Coutu, 1988; Cunjak et al., 1989). In contrast, postsmolts have also been collected from research surveys in the Labrador Sea and indirectly from bird colonies, providing evidence that the extent of the postsmolt migration includes waters north of Newfoundland (Montevecchi et al., 1988; Reddin and Short, 1991). Recoveries of postsmolts in estuarine areas support the hypothesis that specific habitats serve as nursery areas for postsmolts, whereas recoveries in the pelagic zone support the alternative, that juveniles have thermal preferences similar to adults and do not use specific postsmolt nursery areas.

Figure 1

Map of Northwest Atlantic area showing postsmolt habitat for stocks in the Gulf of St. Lawrence and south (horizontal hatching) and sampling area for Gulf of St. Lawrence postsmolts (vertical hatching).

In this paper we re-examined material collected by Dutil and Coutu (1988) with the aim of understanding the use of the Gulf of St. Lawrence by salmon postsmolts. Specifically, we collected circuli spacing data from salmon scales to address the following questions: 1) Are postsmolts retained in the Gulf of St. Lawrence during the postsmolt growth season or are they transient in the area?; and 2) Do postsmolts recovered in the Gulf exhibit growth patterns similar to postsmolts from other stocks? The answers to these questions will hopefully allow us to make some inference about the nature of the nursery for Atlantic salmon and salmonids in general.

Table 1

Sample sizes for circuli analysis by stock group and age of capture.

		Smolt year		
Stock	Age	1982	1983	1984
Connecticut	2SW	52	81	110
Penobscot	1SW	65	63	57
	2SW	75	75	40
St. John	1SW	84	65	51
	2SW	81	67	54
Gulf of St. Lawrence	Post-smolt	372	154	54

Material and methods

We collected scale circuli spacing data representative of postsmolt growth for juvenile salmon captured in the Gulf of St. Lawrence and for three index stocks from the southern portion of the range of salmon in North America. Gulf of St. Lawrence postsmolt salmon were collected in 1982–84 and were originally reported in Dutil and Coutu (1988). These postsmolts were captured in experimental gill nets along the northwest shore of the Gulf during the months from August to October (Fig. 1). Data for comparative purposes come from the returning adults of hatchery origin fish from the Connecticut, Penobscot, and Saint John rivers, all located south of the Gulf of St. Lawrence (Fig. 1). Data for the Connecticut and Penobscot rivers have been presented earlier (Friedland et al., 1996b); whereas, the Saint John data are newly reported here. Sample sizes sorted by smolt year of migration to sea and age of maturity are reported in Table 1. The low number of 1SW returns to the Connecticut River did not provide sufficient samples for inclusion in our study.

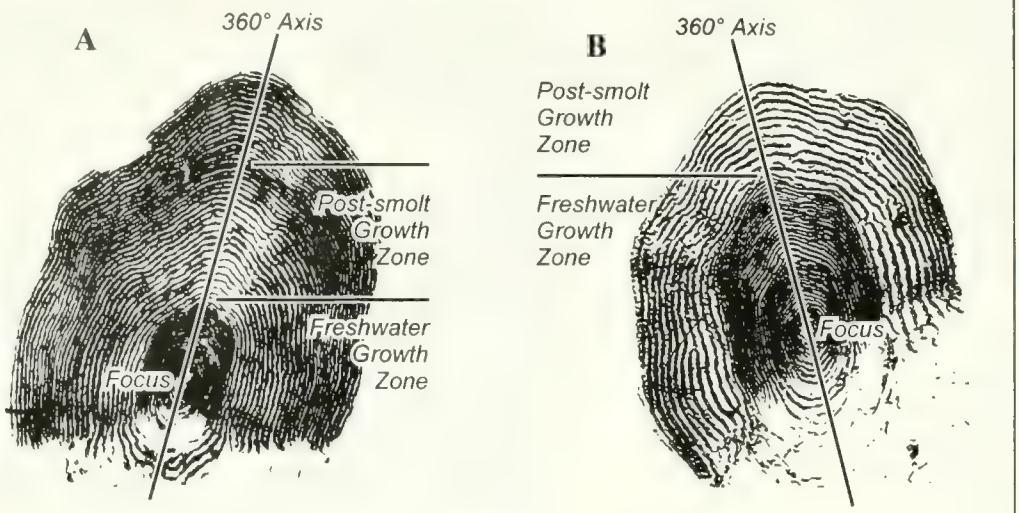

Figure 2

Illustrations of Atlantic salmon scales from a 1SW salmon (**A**) and a postsmolt salmon (**B**). Focus of each scale is marked; freshwater growth zone extends from focus to start of marine growth; and postsmolt growth zone extends to first winter annuli. The figures are not in scale.

Postsmolt growth was interpreted from circuli spacing patterns deposited during the postsmolt year. Scales were cleaned and mounted between glass slides and the spacings of scale circuli were measured with a Bioscan Optimas image processing system. The first spacing was measured between the first circulus of the postsmolt growth zone and the next circulus and continued with successive circuli pairs. For maturing fish returning to their natal river after at least one winter at sea, the measurements were made through the first seawinter annulus of the scale and thus captured the entire postsmolt growth zone (Fig. 2A). For fish captured as postsmolts, measurements were taken to the edge of the scale (Fig. 2B). Thus, only part of the data collected from maturing fish was needed for comparison with the postsmolts. Measurements were made on a single scale from each specimen at a pixel resolution of 0.004 mm along the 360° axis of the scale.

Return rates by sea-age and fraction of the smolt cohort maturing after one seawinter (1SW) were computed for the three stocks used for comparison. Return rates are simple percentages of the number of returns-at-age to the number of smolts released. Return rates for the Connecticut and Penobscot stocks originally reported in Friedland et al. (1996b) are updated here. Return rates for the Saint John stock were computed similarly and are based on smolt releases of 172, 145, and 206 thousand smolts for the years 1982–84, respectively. Releases over the period 1974–92 averaged approximately 200 thousand smolts annually in the Saint John system. The fraction of the smolt cohort maturing after one seawinter, the 1SW fraction, was computed with the formulae of Friedland et al. (1996b). Likewise, these data are updated for the Connecticut and Penobscot stocks and are newly reported for the Saint John stock.

Circuli spacing data for Gulf of St. Lawrence postsmolts were compared in three ways. In the first comparison, data for the postsmolt scales were compared for the period 1982–84. The spacings of the first ten circuli pairs were compared with ANOVA. This and subsequent statistical analyses were restricted to the first ten circuli pairs because most postsmolt scales did not have circuli beyond the tenth pair. As a consequence, spacing patterns for circuli pairs beyond pair number 10 were not well estimated. In the second comparison, for two of the seasons, 1982 and 1983, where sufficient samples of postsmolts were available, samples were poststratified by collection date. The poststratification was done to achieve nearly equal numbers of samples in each stratum. In 1982, three within-year strata were created: 8 to 17 August composed of 126 samples, 18 August to 5 September composed of 121 samples, and 7 September to 18 October composed of 125 samples. In 1983, two strata were created: 24 to 30 September composed of 73 samples and 1 to 11 October composed of 81 samples. Circuli spacing of the first ten circuli pairs for the poststratified groups were compared with ANOVA. For the third comparison, circuli spacing data from Gulf postsmolt scales were compared with the circuli spacing data for the three

Table 2

Results of ANOVAs testing year effect in scale circuli spacing from collections of postsmolt salmon from the Gulf of St. Lawrence from 1982 to 1984.

Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1	2	0.00291	577	0.00015	19.312	0.00	*
2	2	0.00023	577	0.00020	1.170	0.31	
3	2	0.00112	577	0.00024	4.605	0.01	*
4	2	0.00290	577	0.00021	13.491	0.00	*
5	2	0.00591	576	0.00020	28.895	0.00	*
6	2	0.00700	575	0.00017	40.579	0.00	*
7	2	0.00620	574	0.00019	33.492	0.00	*
8	2	0.00482	573	0.00015	31.914	0.00	*
9	2	0.00398	559	0.00016	24.686	0.00	*
10	2	0.00217	526	0.00016	13.521	0.00	*

comparison stocks. The data for the comparison stocks were grouped by sea-age; thus, the postsmolt scale data were compared with a total of five scale growth signals. The statistical comparison was simplified to a two-group ANOVA, namely to comparing circuli spacing of the first ten circuli pairs of the postsmolts with a combined sample of all the comparison stocks.

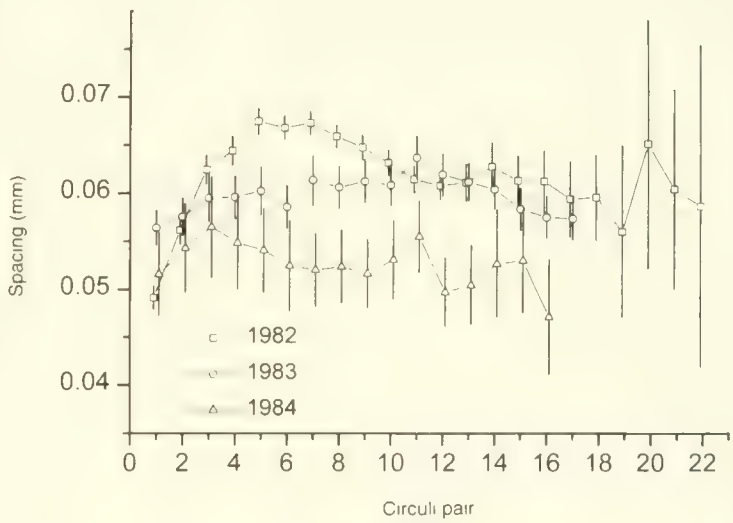

Figure 3

Circuli spacing versus circuli pair for Gulf of St. Lawrence postsmolts for three smolt year classes, 1982–84. Error bars mark 95% confidence intervals.

Results

Circuli spacing patterns for the postsmolt growth zones of Gulf of St. Lawrence postsmolts were significantly different for the three year classes we examined. Circuli spacing for the first few pairs, associated with the first few weeks in the marine environment, were similar in all three years, measuring approximately 0.050 to 0.055 mm (Fig. 3). However, beyond these initial pairs the spacings diverged into three distinct patterns. Spacings for fish captured in 1982, based on the mean spacings for pairs 4–8, were the widest, generally larger than 0.065 mm. Circuli spacings in the same region of the scale were progressively smaller for samples collected in 1983 and 1984. In 1983, most of the mean spacings did not exceed 0.060 mm and for 1984 they did not exceed 0.055 mm. ANOVA results show that the yearly spacings means were significantly different for all but one of the first ten spacing pairs (Table 2). The means for spacing pair number 2 is not significantly different because the rank order of the means changes between spacing pairs 1 and 3.

Within-year comparisons of Gulf of St. Lawrence samples poststratified by collection date suggest that in one year the same group or population of fish were sampled during the entire growth season; whereas, in another year, the postsmolt assemblage appeared to change during the sampling period. All three poststratified groups formed from the 1982 data showed a similar pattern of circuli spacing versus circuli pair through pair number 12 (Fig. 4A). After circuli pair 12, the mean spacing for the three poststratified groups began to diverge; however, the mean spacing for these circuli pairs was estimated

with low precision owing to the small sample sizes available. No significant differences existed between the spacing means for circuli pairs 1–10 (Table 3). In contrast, the data for 1983 showed that spacing patterns and growth were different for early versus late season collections. Fish collected in September had wider circuli spacings for circuli pairs 4–10 than fish collected in October (Fig. 4B). The September samples had mean spacings generally above 0.0625 mm; whereas, the October samples had mean spacings generally below 0.06 mm. Most of the statistical comparisons between the poststratified groups were significant at either P=0.05 or P=0.1 (Table 3).

The seasonal pattern in circuli spacing for Gulf of St. Lawrence postsmolts was similar to the patterns observed for the some of the comparison stocks by year, and dissimilar in other cases. For smolt year 1982, Gulf of St. Lawrence postsmolts and Penobscot and Saint John returns showed similar seasonal patterns of circuli spacing versus circuli pair (Fig. 5A). This comparison included both the 1SW and 2SW maturity groups within a stock. The pattern of mean circuli spacing for Connecticut River 2SW returns was different from that for the other stocks and showed an ontogenetic trajectory of narrower spacings with age. When compared statistically, mean spacings for Gulf postsmolts were significantly higher and lower than the mean for the three comparison stocks (Table 4). The mean spacing for circuli pair 1 was significantly lower for Gulf postsmolts compared with the other stocks, but the relationship between stock circuli spacing changed for pairs 4–8 as the rank order changed. The rank order changed again by circuli pair 10. In 1983, the spacing pattern for the postsmolts could not be distinguished graphically from the combined signals for the other stocks (Fig. 5B), which is supported by statistical comparison as well (Table 4). Again, the Connecticut River stock had the narrowest spacings, whereas the widest spacings were observed in Penobscot and Saint John fish.

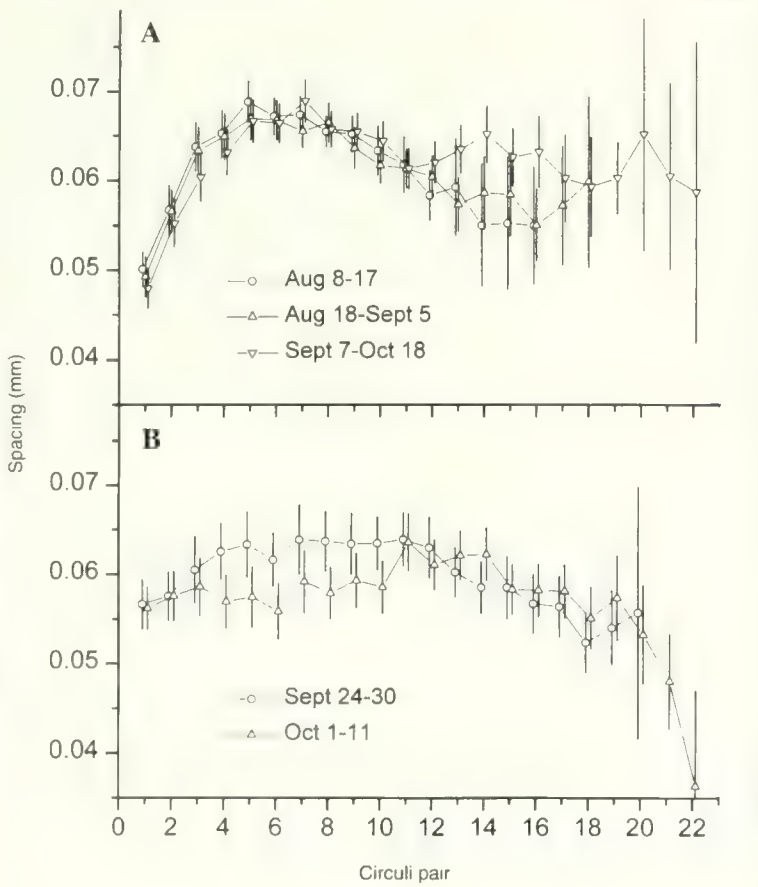

Figure 4

Circuli spacing versus circuli pair for Gulf of St. Lawrence postsmolts for two smolt year classes, 1982 (**A**) and 1983 (**B**). Samples are poststratified by date of capture. Error bars mark 95% confidence intervals.

In 1984, mean circuli spacing varied over a wide range, suggesting the different stocks experienced different growth regimes that year (Fig. 5C). What is particularly striking is that the wild-origin postsmolts from the Gulf had the narrowest mean spacings for most of the postsmolt growth season. Mean spacings for Gulf postsmolts were significantly lower than those for the comparison stocks with the exception of only one spacing pair (Table 4).

The three stocks provided for comparisons with Gulf of St. Lawrence postsmolts displayed a range of return rates and 1SW fraction, reflecting differences in survival and maturity rates. For the Connecticut stock, return rates of 2SW fish and 1SW fraction averaged 0.13% and 0.01, respectively (Table 5). Penobscot River smolts returned at higher rates, 0.09% and 0.47% for 1SW and 2SW fish, respectively. Typically 10% of the Penobscot cohort matured at 1SW. The Saint John stock had the highest return rates and the largest proportion of the cohort maturing after one-seawinter. The return rate for 1SW fish averaged 1.47% and the 1SW fraction averaged 0.59. The 2SW return rate for the Saint John stock is similar to that observed for the Penobscot stock. Thus, the Connecticut stock had the lowest survival rate and produced few early maturing fish; the Saint John stock had the highest survival rate and pro-

duced many early maturing fish; and the Penobscot stock was intermediate between the other two.

Discussion

Our analysis suggests that the role of the Gulf of St. Lawrence as salmon postsmolt nursery habitat varies annually. In some years it appears that the growth of wild postsmolts retained in the Gulf is as robust as and patterned similarly to growth observed for hatchery-origin postsmolts assumed to use open ocean habitats (Reddin and Short, 1991). This correlation suggests that either postsmolts from other areas invade the Gulf and use it as a nursery area or the Gulf region is continuous with a larger area of similar growth conditions where the nursery is formed. In other years, it appears that only smaller, and presumbably less robust, postsmolts remain in the Gulf area and that the nursery was formed elsewhere. Variation in the suitability of nursery habitat must interact with the ability of postsmolts to migrate successfully to more favorable areas. In what was first investigated as a mechanism controlling the return migration of adults, Groot and Cooke (1987) described an analogous situation with the distribution of juvenile sockeye salmon in the Strait of Georgia. It would appear that the dominant wind patterns in the Strait can alter the annual migration of postsmolt sockeye salmon and place them in different nursery areas each year (Peterman et al., 1994). Atlantic salmon postsmolt migration trajectories may be similarly affected. In some years, postsmolts are deposited in areas like the Gulf of St. Lawrence and growth conditions are favorable enough to retain them in the region for the entire season. In other years they are not deposited or retained in the same area. Regardless, our focus shifts to the factors controlling migration and whether they covary with the factors controlling survival.

We view nursery habitat for postsmolt salmon as being dynamically defined because it shifts spatial location on an annual basis to regions where the production will support growth. Many marine fishes use staged distribution separations between estuarine, coastal, and offshore habitats (Blabber et al., 1995). North American origin salmon are generally concentrated in the Labrador Sea as feeding adults or on various migration routes back to their natal rivers as maturing fish (Reddin and Shearer, 1987). However, postsmolt distributions are regulated in part by passive displacement mechanisms and the swim-

Table 3

Results of ANOVAs comparing scale circuli spacing for successive time periods from collections of postsmolt salmon from the Gulf of St. Lawrence during 1982 and 1983.

Year	Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1982	1	2	0.00015	369	0.00014	1.085	0.34	
	2	2	0.00008	369	0.00021	0.365	0.69	
	3	2	0.00036	369	0.00022	1.612	0.20	
	4	2	0.00013	369	0.00021	0.639	0.53	
	5	2	0.00021	369	0.00018	1.167	0.31	
	6	2	0.00002	369	0.00015	0.137	0.87	
	7	2	0.00038	368	0.00014	2.655	0.07	
	8	2	0.00003	368	0.00013	0.215	0.81	
	9	2	0.00017	355	0.00014	1.202	0.30	
	10	2	0.00027	324	0.00015	1.849	0.16	
1983	1	1	0.00001	152	0.00013	0.057	0.81	
	2	1	0.00000	152	0.00015	0.000	0.99	
	3	1	0.00014	152	0.00024	0.582	0.45	
	4	1	0.00120	152	0.00018	6.535	0.01	*
	5	1	0.00133	152	0.00024	5.424	0.02	*
	6	1	0.00129	152	0.00018	6.977	0.01	*
	7	1	0.00084	152	0.00027	3.067	0.08	
	8	1	0.00129	152	0.00019	6.713	0.01	*
	9	1	0.00064	152	0.00021	3.076	0.08	
	10	1	0.00093	152	0.00017	5.412	0.02	*

ming potential of the fish (Reddin and Friedland, 1993). As such, postsmolt migration routes are unlikely to be equivalent among years (Caron, 1983; Jonsson et al., 1993). At some point during the postsmolt's first growing season, swimming ability begins to exceed current velocity and postsmolts can more effectively modify their distribution according to preferences driven by migration mechanisms or foraging behavior. These factors may allow postsmolts to concentrate in specific habitats that best suit their feeding requirements and afford them some measure of protection from predation. However, the process of habitat selection may result in a nursery that encompasses different areas each year and thus not linked to a specific area (Friedland et al., 1996a). Therefore, years of poor feeding and growth conditions in the Gulf of St. Lawrence do not necessarily mean poor survival conditions because they do not preclude the use of other neritic areas as postsmolt nursery. For example, in some years the nursery may form along the south coast of Newfoundland or for that matter make use of few neritic habitats as the fish distribute in offshore areas.

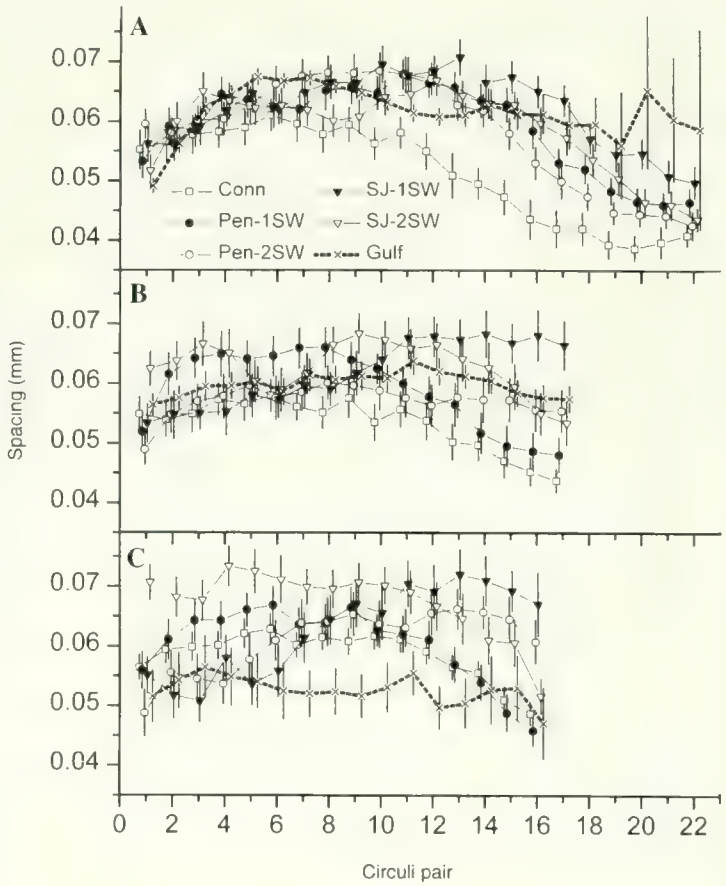

Figure 5

Circuli spacing versus circuli pair for Connecticut 2SW (Conn), Penobscot 1SW and 2SW (Pen), Saint John 1SW and 2SW (SJ), and Gulf of St. Lawrence postsmolts (Gulf) for three smolt year classes, 1982 (**A**), 1983 (**B**), and 1984 (**C**). Error bars mark 95% confidence intervals.

Contemporary characterizations of postsmolt populations may be inadequate if they fail to account for the distribution of postsmolts in neritic habitats. Coherence patterns in the performance of stock complexes has led investigators to search for broad-scale forcing functions to explain variation in returns rate by age (Friedland et al., 1993; Friedland et al., 1998a). In the Northeast Atlantic, a direct link between postsmolt survival and ocean climate has been reported (Friedland et al., 1998a). Spring thermal conditions were associated with the survival of North Sea stocks, which argues that the postsmolt nursery in that region was oceanic and thus directly affected by ocean climate change. However, interpretation of survival signals in the Northwest Atlantic has been complicated by the interplay of mortality and maturation (Friedland et al., 1998b). As the search continues for the factors affecting the survival of Northwest Atlantic postsmolts, investigators must be cognizant of the fact that much of the nursery may occur in inshore neritic waters rather than in pelagic ecosystems and thus may not respond solely to ocean-scale phenomena. This situation may be particularly important in evaluating coastal and offshore predators and how they might be impacting salmon populations. For example, a gannet colony may exert predation pressure over a substantial part of the northern coast of North America; thus, these and other bird species that are adapted to surface prey, such as Atlantic salmon postsmolts, could cause significant predation (Montevecchi and Myers, 1997).

The Gulf of St. Lawrence is a large, complex system that offers a diversity of feeding conditions to smolts upon their entrance into the marine environment. Growth rates would be expected to vary spatially in the Gulf owing to, among other things, highly variable thermal conditions over years. Nursery habitats within the Gulf appear to provide conditions that would support growth rates comparable to those observed in hatchery-reared stocks. But, what clearly differentiates the Gulf habitats from most offshore areas is the rapid continental cooling that occurs in the fall, resulting in an emigration of postsmolts from

Table 4

Results of ANOVAs comparing scale circuli spacing for Gulf of St. Lawrence postsmolts and 1SW and 2SW returns to the Connecticut, Penobscot, and St. John rivers for smolt years 1982–84.

Year	Spacing pair	df effect	MS effect	df error	MS error	*F*	*P*-level	
1982	1	1	0.00702	727	0.00015	47.053	0.000	*
	2	1	0.00057	727	0.00018	3.155	0.08	
	3	1	0.00086	727	0.00020	4.364	0.04	*
	4	1	0.00128	727	0.00018	7.165	0.01	*
	5	1	0.00425	727	0.00017	24.541	0.00	*
	6	1	0.00256	727	0.00015	16.600	0.00	*
	7	1	0.00248	726	0.00015	16.517	0.00	*
	8	1	0.00061	726	0.00015	4.086	0.04	*
	9	1	0.00001	713	0.00015	0.081	0.78	
	10	1	0.00081	682	0.00017	4.872	0.03	*
1983	1	1	0.00050	503	0.00016	3.117	0.08	
	2	1	0.00000	503	0.00019	0.004	0.95	
	3	1	0.00001	503	0.00021	0.029	0.87	
	4	1	0.00001	503	0.00023	0.032	0.86	
	5	1	0.00005	503	0.00022	0.232	0.63	
	6	1	0.00003	503	0.00020	0.156	0.69	
	7	1	0.00018	503	0.00021	0.873	0.35	
	8	1	0.00002	503	0.00018	0.093	0.76	
	9	1	0.00006	503	0.00020	0.277	0.60	
	10	1	0.00000	503	0.00020	0.002	0.97	
1984	1	1	0.00168	364	0.00018	9.118	0.00	*
	2	1	0.00125	364	0.00020	6.302	0.01	*
	3	1	0.00052	364	0.00022	2.396	0.12	
	4	1	0.00327	364	0.00020	11.568	0.00	*
	5	1	0.00336	363	0.00020	16.552	0.00	*
	6	1	0.00552	362	0.00022	25.136	0.00	*
	7	1	0.00551	362	0.00015	35.738	0.00	*
	8	1	0.00606	361	0.00016	39.032	0.00	*
	9	1	0.00783	360	0.00016	48.985	0.00	*
	10	1	0.00512	358	0.00017	31.024	0.00	*

Table 5

Percent return rate by age group and 1SW fraction for three hatchery index stocks. Return rates are in percent where fraction is proportion of cohort maturing after one sea-winter. Mean is for the period smolt years 1974–92.

Smolt year	Connecticut		Penobscot			St. John		
	2SW	Fraction	1SW	2SW	Fraction	1SW	2SW	Fraction
1982	0.02	0.00	0.05	0.52	0.08	0.91	0.65	0.49
1983	0.30	0.02	0.05	0.66	0.06	1.00	0.61	0.54
1984	0.09	0.00	0.04	0.59	0.04	0.98	0.39	0.59
Mean	0.13	0.01	0.09	0.47	0.12	1.47	0.57	0.59

the region (Dutil and Coutu, 1988). The northern Gulf can cool to temperatures below 2°C by late November and to lethal temperatures later in winter, from the surface to a depth of 100 m. Thus, the Gulf must be viewed as a seasonally transient habitat for postsmolts in most, if not all, years.

Our comparisons of growth patterns could be enhanced with the inclusion of growth information from stocks originating in the Gulf of St. Lawrence itself. We assumed that the range of growth patterns provided by the three comparison stocks is representative of stocks outside the Gulf region. However, the samples failed to account for growth signals from wild stocks and included only populations from the southern portion of the range. However, the strength of the sample is that it did include three stocks of varying growth and survival characteristics, thus supporting the contention that it likely represents a range of growth responses similar to those occurring in wild stocks.

A future challenge for research would be to characterize the thermal properties and production characteristics of the area potentially comprising the postsmolt nursery to evaluate its spatial and temporal extent and annual variability. From these descriptive analyses, it may be possible to design migration simulations and field experiments that could begin to describe the mechanisms that form the postsmolt nursery and, in turn, it may be possible to develop an understanding of the factors affecting postsmolt survival and recruitment in salmonid populations.

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Abstract.—Using improved indices of age-1 recruitment and parent stock, I investigated the existence of a stock-recruitment relationship for ocean shrimp, *Pandalus jordani*. I also examined the effects of large catches of egg-bearing shrimp in April on subsequent recruitment. After known environmental influences were accounted for, regression analysis revealed evidence of a quasilinear relationship between recruitment and either spawning stock or egg production. The stock-recruitment relationship showed that average recruitment increases if higher spawner abundance is maintained in years of low abundance. The recruitment-stock relationship, however, showed that low abundance of spawning fish was mostly a result of environmentally driven recruitment failures, rather than just fishery impacts. Fishing did contribute to the low numbers of spawning fish in 1993, and catches of egg-bearing shrimp in April 1989 may have also depressed the 1990 year class. The strong recruitment-stock relationship for ocean shrimp suggests that an increase in escapement of all ages of shrimp in response to a year-class failure may do more to bolster recruitment than traditional strategies aimed at protecting age-1 shrimp.

A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock-recruitment relationship

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Recruitment of the ocean shrimp, *Pandalus jordani*, to the fishery in waters off Oregon has been shown to be influenced strongly by ocean conditions during early larval stages (Hannah, 1993). Specifically, sea level height (SLH) during the month of April, shortly after the bulk of larval release, is strongly negatively correlated with recruitment of age-1 shrimp to the fishery the following year (Hannah, 1993). Although the mechanism linking recruitment to April SLH remains unclear, April SLH probably integrates the strength and timing of the spring transition in coastal currents (Huyer et al., 1979). Ocean shrimp larvae inhabit the near-surface waters shortly after release, occupying progressively deeper strata as they develop (Rothlisberg, 1975; Rothlisberg and Miller, 1983). The nature of the spring transition probably influences the alongshore transport of early larvae, as well as the nearshore temperature regime, either of which could strongly influence shrimp larval survival (Rothlisberg, 1975; Rothlisberg and Miller, 1983; Hannah, 1993; McConnaughey et al., 1994).

Attempts to relate ocean shrimp recruitment to the size of the parent spawning stock, even allowing for the influence of April SLH, have been unsuccessful (Abramson and Tomlinson, 1972; Gotshall, 1972; Geibel and Heimann, 1976; Hannah, 1993). Efforts to date have, to a large degree, relied on assumptions of constant catchability and natural mortality. Recently, both natural mortality rates and the catchability coefficient have been shown to be quite variable for ocean shrimp (Hannah, 1995). I have suggested previously that variation in catchability and natural mortality may have created large enough errors in prior indices of shrimp stock and recruitment as to obscure an underlying relationship between these two variables (Hannah, 1995). In the present study, new indices of ocean shrimp recruitment and spawning stock were developed which do not rely, or rely only very minimally, on assumptions of constant catchability and natural mortality. The main objective of this study was to re-examine the relationship between shrimp recruitment and both shrimp spawning stock and April SLH in the year of larval release, using these improved indices.

Another problem with earlier studies of ocean shrimp stock size and recruitment is that they have relied on measures of parent stock or spawning biomass, rather than on more direct measures of reproductive output, such as estimates of

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egg production (Rothschild and Fogarty, 1989; Hannah et al., 1995). A second objective of this study was to construct, in addition to an improved index of spawning stock, an index of egg production, and evaluate the relationship between recruitment and egg production. One of several challenges in constructing such an index is that the trawl fishery harvests egg-bearing female shrimp in late October, just before the fishing season ends, and again in early April, as fishing resumes. It can be argued that because of reduced fishing effort late in the season in most years and because of the high natural mortality rates experienced by ocean shrimp over the winter, the harvest of egg-bearing shrimp in October should have a negligible impact on total larval release the next spring. However, in April, when larval release is imminent for any shrimp still bearing eggs, the impact of the fishery could be more detrimental. Also, with much of the larval release taking place before the fishing season opens on 1 April, fishery impacts are concentrated on late-release larvae. If, as postulated in the prior study (Hannah, 1993), the timing of the spring transition is critical to larval survival or retention in the study area, the fishery may be impacting the larvae with the greatest chances for success in a poor environment: those destined for release after a late spring transition. A third objective of this study was to estimate the harvest of egg-bearing shrimp in April and examine the impact that April harvest of egg-bearing shrimp may have had on subsequent recruitment.

Materials and methods

In my earlier study of ocean shrimp stock and recruitment (Hannah, 1993), I used an age-structured index of recruitment calculated by summing two components. The first component was an estimate of the age-2 shrimp population in April (year t), calculated from the average fishery catch per unit of effort (CPUE) of age-2 shrimp in April and May, divided by an assumed catchability coefficient calculated from data in Geibel and Heimann (1976). The second component was simply a sum of the catch of age-1 shrimp during the prior year (t–1), with each monthly catch discounted to 1 April of year t by using an assumed monthly natural mortality rate of 0.096 (Gotshall, 1972). In essence, this index was a crude estimate of what the age-2 shrimp population would have been in the absence of fishing, on 1 April of the age-2 year (Hannah, 1993). To index the shrimp spawning stock in the earlier study, I used a simple average of September–October shrimp fishery CPUE. Both indices depended heavily on an assumption of constant catchability. The recruitment index also relied on an assumption of constant natural mortality.

The relationship between CPUE, population size, geographic stock area, and the catchability coefficient can be described by the equations

$$CPUE = paNA^{-b} \quad (1)$$

$$q = paA^{-b}, \quad (2)$$

where p = the proportion of shrimp within the sweep of the gear that will be captured (the elemental efficiency);
A = the geographic stock area (stock area);
a = the area covered by a single sweep of the gear;
b = a coefficient that describes how q will vary with stock area;
N = the population size; and
q = the catchability coefficient (Winters and Wheeler, 1985).

Accordingly, an assumption of constant catchability is equivalent to assuming that stock area is constant. However, stock area for ocean shrimp has been shown to be roughly proportional to stock abundance and to vary substantially between years (Hannah, 1995; Hannah, 1997). In the present study, I incorporated stock area estimates into both the shrimp recruitment and spawner indices, making an assumption of constant catchability unnecessary. I did assume that b in the above equation was equal to 1, an assumption that has been previously shown to be reasonable, according to a roughly linear relationship between stock area and abundance (Hannah, 1995). My approach also assumes that the elemental efficiency of shrimp trawl gear, p, is constant.

Because the assumed rate of natural mortality was used in the prior study (Hannah, 1993) only to discount age-1 catches forward in time to 1 April of the age-2 year, the simplest way to reduce the influence of variable natural mortality on the recruitment index is to index the population at an earlier age. This is a useful approach; however, age-1 shrimp must still be fully recruited to the fishery at the time chosen. Using data from the early years of the shrimp fishery, Lo (1978) showed that age-1 shrimp were incompletely recruited to the California shrimp fishery, especially early in the April–October season. A variety of data suggest that, since about 1979, age-1 shrimp have been fully recruited to the trawl fishery by June or July of each year. Prior to 1974, Oregon required a minimum codend mesh of 34.9-mm (1 3/8 in) stretch measure. Since this date, minimum codend mesh size has been unregulated in the Or-

egon fishery, although California still requires a minimum codend mesh of 34.9 mm. Prior to 1978, shrimp growth was slower (Hannah and Jones, 1991) and age-1 shrimp in the study area (Fig. 1) were clearly not fully recruited to trawl gear until very late in the season (ODFW[1]). After 1978, shrimp growth increased, possibly owing to reduced density from heavy fishing, although other factors were also involved, notably accelerated sex change that may have been a response to reduced numbers of older shrimp (Charnov et al., 1978; Hannah and Jones, 1991). Average codend mesh size in the Oregon fleet also decreased sometime during the 1970s, averaging 30.2 mm by 1981, decreasing to 28.7 mm by 1991–92 (Jones et al., 1996). Accordingly, in this study I chose the August–September time period to index the age-1 shrimp population, and restricted my analysis to the years after 1979. With the months of August–September, the population was indexed eight months earlier than in the previous study, but at a time period late enough that age-1 shrimp could reasonably be assumed to be fully recruited to the trawl gear being fished.

To index shrimp recruitment in the present study, I used the average August–September CPUE for age-1 shrimp only as an index of density and multiplied this index by stock area (ha) for the same year class (Hannah, 1997). In this case, CPUE was expressed as shrimp per hectare trawled, using an average estimate of 5.93 ha trawled per single-rig equivalent hour fished (Hannah, 1995). To account for years in which early season catches of age-1 shrimp were high, I added in the catch of age-1 shrimp for the months of April–July of the same year. Thus, recruitment was calculated as

$$R_t = (D_t A_t) + C_t, \quad (3)$$

where R = recruitment of age-1 shrimp in year t;
D = the average fishery CPUE of age-1 shrimp in August and September of year t;
A = the stock area for the age-1 year class in year t; and
C = the summed fishery catch of age-1 shrimp in the months April to July of year t.

Use of these additional catches for April–July does rely on an assumption of constant natural mortality, although the importance of this assumption is clearly reduced. Age-1 shrimp CPUE for Pacific States Marine Fisheries Commission (PSMFC) statistical areas 82–88 was obtained from Zirges et al. (1982) and Hannah et al. (1997). The collection and analysis of biological samples from the commercial catch has been described by Hannah and Jones (1991).

[1] ODFW (Oregon Department of Fish and Wildlife). 1981 to present. 2040 SE Marine Science Dr., Newport, OR. Unpubl. data.

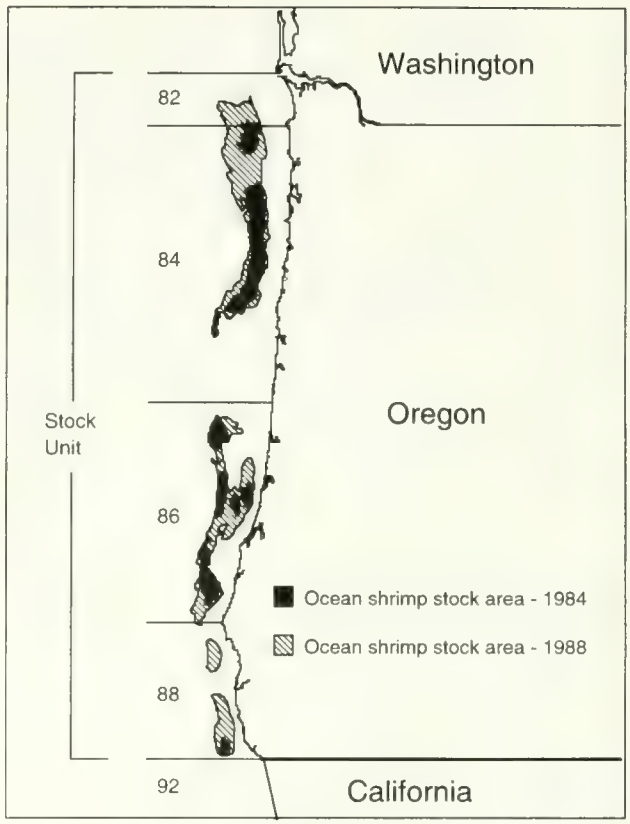

Figure 1

Location of commercial concentrations of ocean shrimp (*Pandalus jordani*) off coastal Oregon, in Pacific States Marine Fisheries Commission statistical areas 82–88. Dark areas show the approximate minimum areal extent of the shrimp grounds (1984) and the lighter shaded areas show the largest areal extent observed from 1980 to 96 (1988).

The data used to construct the recruitment and spawning stock indices developed in this study differ in some respects from the data used for the prior recruitment study. In the prior study, logbook data were available from Washington, Oregon, and California, such that a complete accounting of catch and effort was possible for PSMFC areas 82–92 (Fig. 1). Beginning in 1992, logbook data from the states of California and Washington became unavailable. Accordingly, the data used in this study was based on Oregon landings for the entire study period. To minimize the impact of the missing information on the indices developed, the study area was limited to areas 82–88 (Fig. 1). I believe that the missing information will create very minimal error in the new indices for several reasons. First, Oregon landings comprise the great majority of the removals of shrimp from statistical areas 82–88. The average percent-

age of total catch from these areas landed in Oregon from 1980 to 1992 was 92.5% (Hannah et al., 1997). Second, the components of the new indices, with one exception, did not depend on a complete accounting of catch and effort from the study area but simply on a good estimate of average CPUE at age and accurate estimates of stock area. The one component of the recruitment index that was somewhat influenced by the missing catch data was the added age-1 shrimp catch from the months of April–July. A correction for this potential source of error is not available; however, I believe the magnitude of error introduced is likely to be small in relation to the interannual variation in the index itself.The use of CPUE as a direct index of density is equivalent to assuming that elemental efficiency, p in Equation 2 above, equals 100%. This is clearly not reasonable, however; selecting a value for p is problematic. The principal importance of selecting a value for p is to obtain a proper scaling between the two components of the recruitment index: one based on CPUE and stock area; the other based on the early-season catch of age-1 shrimp. Proper scaling of these two components is less critical than it seems at first examination because the two index components are actually closely correlated (r=0.774 at p=0.5). Accordingly, a change in the scaling between the two components is expected to have little influence on the pattern of time series variation in the resulting index. As a check on this assumption, all indices using CPUE as a density index in this study were calculated with a range of p-values, and the results were then examined to see if they were sensitive to assumptions about p. For the primary analysis, I chose a p-value of 0.5 and for the sensitivity analysis I used values of 0.25 and 0.75. for p, following my earlier examination of shrimp mortality rates (Hannah, 1995).

Commercial logbook data were used to generate estimates of stock area for each shrimp year class. The methods used to estimate stock area, including the correction of estimates for variation in sampling rates, are described in detail in Hannah (1997). Stock area was estimated by using logbook data from June of the recruit year through May of the following year, the time period during which age-1 shrimp contribute most heavily and reliably to the catch. For a few of the years in the 1980–96 time series, the fishery failed to target age-1 shrimp adequately, and harvested primarily the remaining age-2 and older shrimp from prior year classes. For those years, stock area was estimated from a linear regression of stock area on a simple virtual population estimate for that year class, as described in Hannah (1997).

To index the ocean shrimp spawning stock, I used an approach similar to that used for the recruitment index. For each spawning year, I used the average age-specific CPUE in September–October as an index of age-specific density. Once again, these estimates of density were expanded by using assumed levels of elemental trawl efficiency ranging from 0.25 to 0.75, as discussed above. I then multiplied each density index by the stock-area estimate for that year class, as calculated in the year of recruitment. In using this approach I assumed that the geographic distribution of each newly recruited year class was established at settlement and was persistent, and that local shrimp density was modified by fishing and natural mortality. This assumption is supported by several observations, including the obvious autocorrelation in stock area estimates noted previously (Hannah, 1995), the lack of any evidence for migration in this species and the approximately linear relationship between stock area and abundance. There is some evidence from sea bed drifter recoveries (ODFW[1]) that suggests slow gyres in bottom currents may help retain or concentrate shrimp in some of the major shrimp beds. However, it is unknown whether this effect is sufficiently large to actually alter the areal extent of a shrimp year class after settlement.

An egg production index for ocean shrimp was calculated by expanding the spawner index with available shrimp biological data (ODFW[1]). The biological data used included the mean percentage of females and mean female shrimp carapace length, by age, from samples of the fishery in October. For a few years, October samples were unavailable and September samples were used. I used a pooled length-fecundity relationship from Hannah et al. (1995) to estimate mean fecundity for each age group of female shrimp based on mean carapace length data.

The April harvest of egg-bearing females was estimated for the years 1979–95 in a straightforward manner. April shrimp catch, expressed as numbers of shrimp, for each PSMFC statistical area, was obtained from Hannah et al. (1997). Catch in numbers was multiplied by the average percentage of egg-bearing shrimp estimated for each PSMFC area from biological samples of the April catch (ODFW[1]). The catch of egg-bearing shrimp from each of the four areas (Fig. 1) was then summed.

Because the percentage of egg-bearing shrimp declined throughout April, a time-stratified approach was used to estimate the average percentage of egg-bearing shrimp. One problem with this approach is variation in sample coverage. Although the total number of shrimp examined from the April catch has been fairly consistent, averaging about 2900 shrimp from 1980 to 1996, the early and late portions of April have not always been sampled evenly. For example, some years that had excellent sample coverage in

the first two weeks of April had no samples at all for the second half of the month. To make maximum use of the data available, estimates of the percentage of egg-bearing shrimp from individual samples were averaged for the first and second halves of the month, respectively. These semimonthly figures were then averaged to produce an overall mean percentage of egg-bearing shrimp in the catch for each April. When samples were missing from the latter half of the month, a zero level of ovigerous shrimp was assumed. When samples were missing for the first half of the month, the level of ovigerous shrimp observed for the second half was assumed as a minimum estimate for the first half of April. Accordingly, the estimates presented in the present study are minimum estimates of the catch of egg-bearing shrimp.

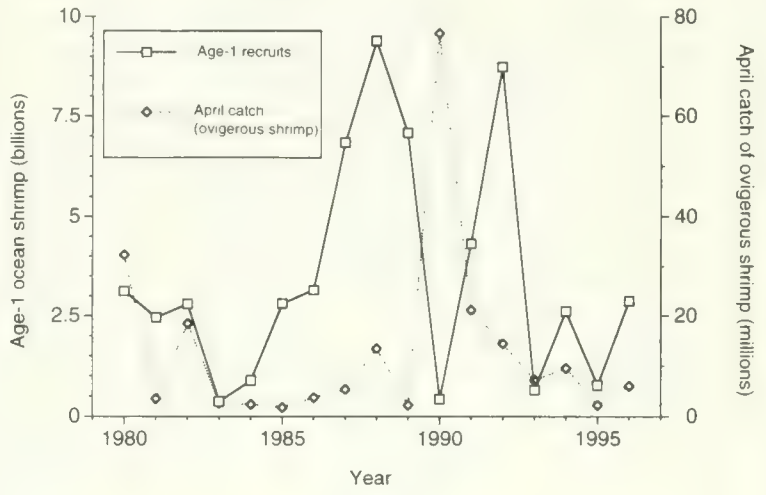

Figure 2

Time series of the recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the fishery catch of egg-bearing shrimp from April of the year of larval release, by year of age-1 recruitment, 1980–96.

To determine when, during the month of April, egg-bearing shrimp had declined to a minimal component of the catch, I constructed a scatter graph of the raw percentages of egg-bearing females by date, using existing data for 1961–97 (ODFW[1]). Area 82 (Fig. 1) was excluded from this analysis because the incidence of egg-bearing shrimp in this area was generally very low in April.

A stepwise process was used to evaluate the relationships between the new recruitment, spawner, and egg production indices, calculated at assumed values of 0.25., 0.50 and 0.75 for trawl efficiency. Following the findings of my earlier study (Hannah, 1993), the first step in this analysis was to regress log (natural log unless noted) recruitment against April SLH at Crescent City, California, to verify that SLH still explained a significant amount of the interannual variation in recruitment. Simple linear regression was used for this test. These SLH data were obtained from the National Oceanic and Atmospheric Administration's Ocean and Lake Levels Division for the years 1979–95, corresponding to age-1 catch years 1980–96. Next, the residuals were examined and compared graphically and by means of linear regression to the spawner and egg production indices, and outliers were examined in light of the estimates of the catch of egg-bearing shrimp in April. Finally, some multivariate models incorporating April SLH and the spawner and egg production indices were fitted by using multiple regression.

Garcia (1983) and others have stressed that many of the stock-recruitment relationships that have been demonstrated for shrimp stocks are really statistical artifacts caused by a strong recruitment-stock relationship (the reverse of a stock-recruitment relationship, rather spawning stock in year t as a function of recruitment that same year) in combination with serially autocorrelated, environmentally driven, recruitment. To test for such a possibility in the present analysis of ocean shrimp recruitment, I regressed the new recruitment index against itself at a lag of one year. I also examined the recruitment-stock relationship further by graphically comparing the spawning index, broken out by age class, to the recruitment index from the same year.

Results

The recruitment index (Fig. 2; Table 1; all indices calculated assuming 0.50 for trawl efficiency, unless noted) shows wide variation in ocean shrimp recruitment, especially after 1986 (year of age-1 recruitment, unless noted). Recruitment in 1983, 1984, 1990, and 1993 was very low, whereas very high recruitment was observed for the 1987–89 and 1992 year classes. These four large year classes had a very significant influence on total landings from the shrimp fishery during the years included in this study. Although they represent less than one third of the years in the time series, they contributed roughly 60% of the total landings of shrimp.

The log of the shrimp recruitment index was stongly negatively correlated with April SLH at Crescent City, California, in the year of larval release

Table 1

Ocean shrimp population data used for regression analyses, including April SLH, geographic stock area (year is June–May), and recruitment, spawner, and egg production indices, by calendar year (no lags). Recruitment, spawner, and egg production indices are calculated assuming elemental trawl efficiency of 0.50.

Year	Recruitment index (millions — age 1)	April SLH (cm)	Geographic stock area (1000 ha)	Spawning abundance (millions)	Egg production (billions)
1979	—	214.9	—	—	—
1980	3122.0	218.2	450.6	—	—
1981	2455.0	210.9	477.2	—	—
1982	2789.1	226.5	344.1	2133.0	2002.9
1983	368.6	229.2	172.9	604.0	717.1
1984	884.5	211.5	158.7	1150.7	1257.4
1985	2798.4	213.1	319.4	3049.7	1913.4
1986	3148.7	212.5	460.5	2293.1	1616.0
1987	6840.2	209.1	464.6	3760.3	2558.0
1988	9388.1	214.9	605.0	7332.6	5783.8
1989	7078.9	222.2	585.1	6872.6	4845.5
1990	429.2	219.2	208.8	1652.2	3583.3
1991	4312.5	212.5	478.1	2141.4	1590.4
1992	8729.9	230.7	406.3	4519.7	4146.1
1993	649.9	227.4	200.8	921.4	1670.2
1994	2608.4	215.0	364.1	1465.3	1291.0
1995	768.6	220.0	215.7	—	—
1996	2862.8	—	362.0	—	—

(Fig. 3). The linear regression model (Table 2; model 1) was highly significant, with April SLH explaining 48% (unadjusted for degrees of freedom, unless noted) of the variation in log recruits. More importantly, the linear relationship is not based heavily on just a few points but appears quite general in nature, confirming a routine relationship between recruitment and April SLH shortly after the peak of larval release.

The residuals from the regression of log recruits on April SLH, graphed against the spawner index, show a pattern that is suggestive of a quasilinear stock-recruitment relationship, with the 1990 year class as an exceptional outlier (Fig. 4). The same residuals regressed against the egg production index show a similar pattern (Fig. 5). The time series of recruitment and the April catch of egg-bearing shrimp from the year of larval release (Fig. 2) shows that the year class released in 1989 (1990 year class) may have been heavily impacted by the trawl fishery, owing to an extremely high harvest of late egg-bearing shrimp. This occurred in combination with a high April sea level, suggestive of a late spring transition (Table 1). Data on the percentage of ovigerous females in the April catch (Fig. 6) suggest that postponement of the opening of the season to April 20th each year could eliminate this impact.

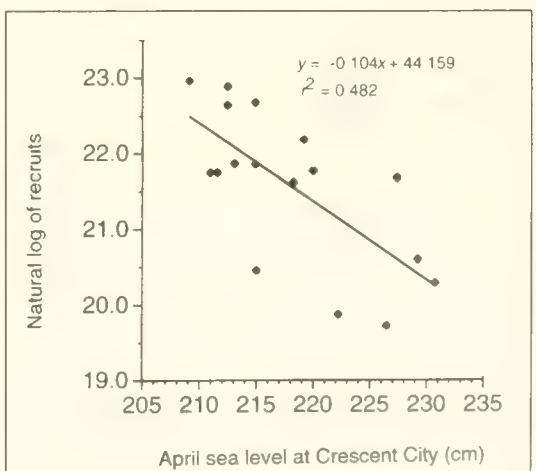

Figure 3

Linear regression of the natural log of the shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, versus mean sea level height at Crescent City, California, during April of the year of larval release.

When the 1990 year class was excluded, neither scatter graph (Figs. 4–5) exhibited sufficient evidence of curvature to indicate the most appropriate form

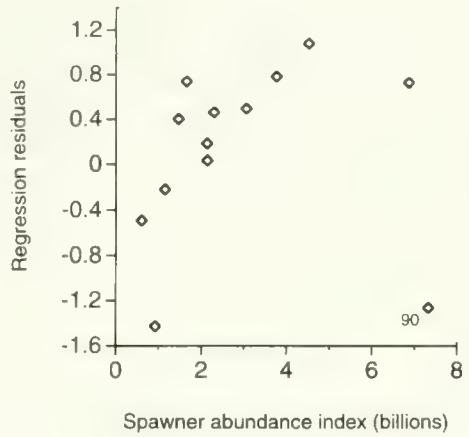

Figure 4

Residuals from regression of ln(recruits) on April SLH at Crescent City, California, versus the ocean shrimp spawner index from the parent year. Both indices were calculated assuming elemental trawl efficiency of 0.50.

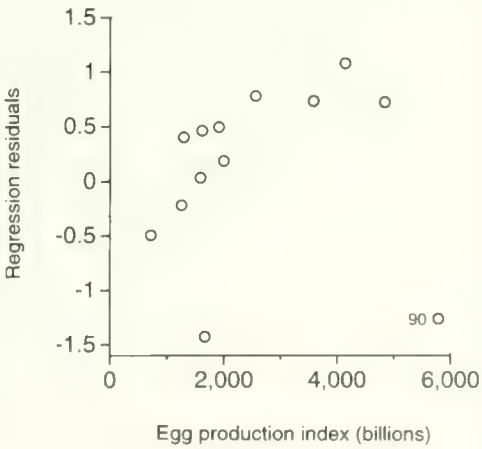

Figure 5

Residuals from the regression of ln(recruits) on April mean sea level height at Crescent City, California, versus the ocean shrimp egg production index from the parent year. Both indices were calculated assuming elemental trawl efficiency of 0.50.

of the stock-recruitment relationship for ocean shrimp. If the 1990 year class was included, the graphs could be interpreted as supporting a dome-shaped stock-recruitment curve, or could even be interpreted as evidence of no relationship between stock and recruitment at all. Given the extremely large fishery impact on egg-bearing females in the

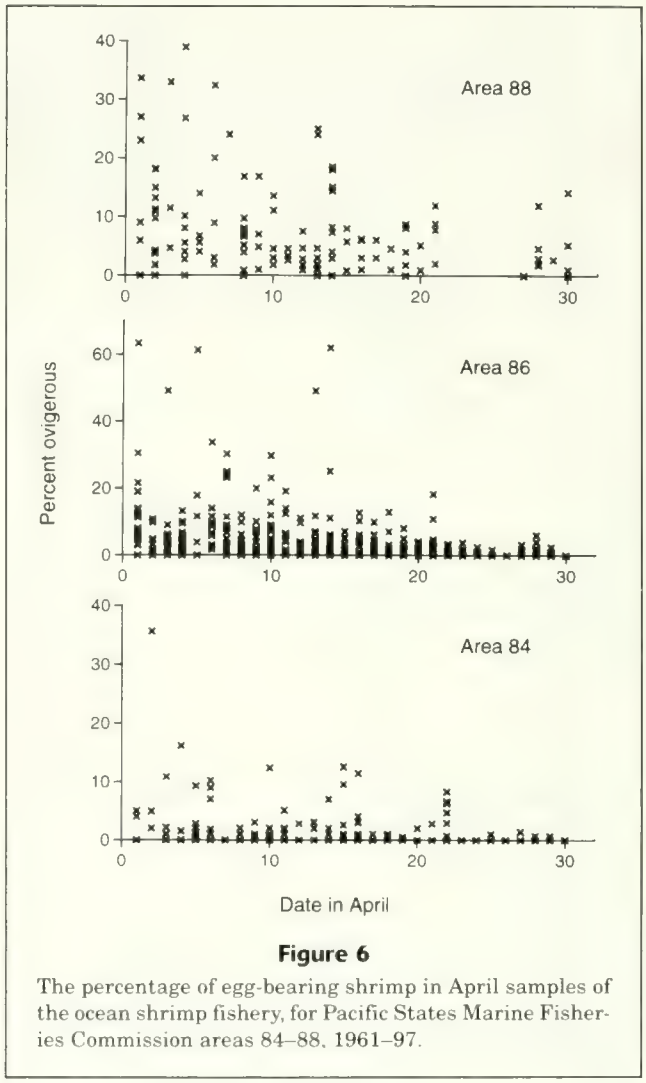

Figure 6

The percentage of egg-bearing shrimp in April samples of the ocean shrimp fishery, for Pacific States Marine Fisheries Commission areas 84–88, 1961–97.

spring of 1989 (Fig 2), in combination with the fact that April has been shown to be a critical period for larval survival, excluding the 1990 data point seems the most conservative approach. With the 1990 year class excluded, a multivariate model incorporating April SLH and the log of the spawner index, was highly significant ($P<0.001$) and explained 79% of the variation in log recruitment (Table 2, model 2). The comparable multivariate model, incorporating the egg production index, was also highly significant ($P<0.01$) and explained 68% of the variation in log recruitment (Table 2, model 3). Both models incorporated April SLH and log spawners or eggs with negative and positive slopes, respectively. A linear regression of the recruitment index on itself, at a lag of one year, was nonsignificant ($P>0.05$) and showed little evidence of serial autocorrelation, suggesting that the evidence presented in Figures 4 and 5, for a statistical dependence of recruitment on parent stock in ocean shrimp, may be valid.

Table 2

Results of univariate and multivariate regression analysis. Dependent variable is the natural log of the ocean shrimp recruitment index in year t. All population indices are calculated assuming elemental trawl efficiency of 0.50.

Parameters and variables	Coefficients	95% CI	F-value	R^2 (adjusted)	$P>F$
Model 1					
Intercept	44.159				
April SLH_{t-1}	–0.104	±0.059			
Full Model			13.983	0.448	0.0020
Model 2 (1990 excluded)					
Intercept	29.108				
April SLH_{t-1}	–0.112	±0.047	29.388		0.0004
Ln (spawner index)$_{t-2}$	0.796	±0.502	12.893		0.0058
Full Model			16.550	0.739	0.0010
Model 3 (1990 excluded)					
Intercept	21.636				
April SLH_{t-1}	–0.103	±0.056	17.528		0.0024
Ln(egg index)$_{t-2}$	0.799	±0.754	5.743		0.0401
Full Model			9.676	0.612	0.0057
Model 4					
Intercept	27.531				
April SLH_{t-1}	–0.119	±0.053	26.037		0.0006
Ln(spawner index)$_{t-2}$	0.957	±0.628	11.879		0.0073
April catch of ovigerous Shrimp$_{t-1}$ (millions)	–0.035	±0.022	13.006		0.0057
Full model			11.956	0.733	0.0017

A multivariate model, using the complete data series and incorporating April SLH, the natural logarithm of the spawner index, and the April catch of egg-bearing shrimp from the year of larval release, was also highly significant ($P<0.005$) and explained 80% of the variation in log recruitment (Table 2, model 4). As expected, the coefficients for SLH and the catch of egg-bearing shrimp in April of the release year were both negative, whereas the coefficient for the natural logarithm of spawners was positive. Fitting this three-variable model, with the 1990 year class excluded, resulted in the catch of egg-bearing shrimp not contributing significantly to the overall model fit, suggesting that this variable does not have general predictive value for the recruitment time series but is useful only in explaining the very low recruitment in 1990.

Despite efforts to de-emphasize the importance of age-1 catches in the recruitment series by indexing the stock at an earlier age, these early catches still represented a large component of the index (Fig. 7). This finding suggests that the assumption of constant natural mortality could still be inducing errors in the recruitment index. However, when the analyses discussed above were conducted on the recruitment index excluding the April–July age-1 catches, the results were very similar. This similarity argues that the findings of this study are not sensitive to failure of the assumption of constant natural mortality, as it is employed in calculating the recruitment index. The results were also insensitive to the assumed level of elemental trawl efficiency (Table 3, models 5 and 6).

The data in Figure 4 suggest that if shrimp spawner abundance could be maintained above some threshold (about 1.3 billion shrimp for an assumption of 0.50 for elemental trawl efficiency), the ability to produce large shrimp year classes in favorable environmental conditions could be preserved in all years. A similar threshold could also be identified in terms of egg production (Fig. 5). Examination of the relationship between age-1 spawners, older spawners, and the recruitment index from the same calendar year (Fig. 8), suggests a strong recruitment-stock relationship for ocean shrimp and a minor role for the fishery in determining spawner abundance. In

Table 3

Results of multivariate regression analysis using alternative assumed values for elemental trawl efficiency. Dependent variable for models 5 and 6 is the natural log of the ocean shrimp recruitment index in year t, calculated assuming elemental trawl efficiency of 0.25 and 0.75, respectively.

Parameters and variables	Coefficients	95% CI	F-value	R^2 (adjusted)	$P>F$
Model 5 efficiency of 0.25					
Intercept	27.583				
April SLH_{t-1}	−0.122	±0.056	24.306		0.0008
Ln (spawner index)$_{t-2}$	0.976	±0.666	11.022		0.0089
April catch of ovigerous Shrimp$_{t-1}$ (millions)	−0.038	±0.024	13.252		0.0054
Full model			11.500	0.724	0.0020
Model 6 efficiency of 0.75					
Intercept	27.437				
April SLH_{t-1}	−0.117	±0.051	26.829		0.0006
Ln (spawner index)$_{t-2}$	0.946	±0.608	12.378		0.0065
April catch of ovigerous Shrimp$_{t-1}$ (millions)	−0.034	±0.022	12.683		0.0061
Full model			12.107	0.735	0.0016

each of the years in which spawner abundance falls below the proposed threshold, there was a serious recruitment failure, depressing the age-1 population. In the case of spawn-year 1984, two year-class failures in a row were evident. All of the very low year classes shown in Figure 8 coincide with high April SLH the prior year (Table 1), suggesting that most low spawner abundances were largely the result of environmental forcing and a strong recruitment-stock relationship. Two of the years shown, 1984 and 1993, followed the major El Niño southern oscillation (ENSO) events of 1982–83 and 1992–93, and likely resulted from the rise in sea levels and accelerated northward currents often associated with these events and their likely influence on conditions in April (Huyer et al., 1979; Chelton and Davis, 1982; Chelton et al., 1982; Huyer and Smith, 1985).

Figure 7

Age-1 ocean shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the portion of the index for the April–July catch of age-1 shrimp, by year, 1980–96.

However, the data suggest that the fishery does play some role in creating the low spawner abundances shown in Figure 8. Although the low recruitment in 1990 corresponds to a poor spring transition in 1989 (Table 1), the data suggest that the high harvest of egg-bearing females in April of 1989 exacerbated this recruitment failure (Fig. 2; Tables 1 and 2), subsequently depressing spawner abundance (Fig. 8). The large difference between age-1 recruitment and the age-1 component of the spawner index in 1993 (Fig. 8) also suggests that spawner abundance may have been depressed by the fishery in that year. The close association between a year-class failure and low spawning abundance the same year also demon-

strates that attempting to maintain a spawner threshold by increasing escapement of age-1 shrimp is unlikely to be an effective management strategy. The reason for this is that precisely when a boost in spawner abundance is needed, the age-1 year class is too depressed to offer significant help, even with a complete cessation of fishing. This result suggests that when a year-class failure is detected in this stock, reducing fishery impacts on all age classes of shrimp may be a better strategy to maintain spawner abundance than the standard management measures (e.g. mimimum codend mesh or maximum count per pound) which protect the escapement of age-1 shrimp.

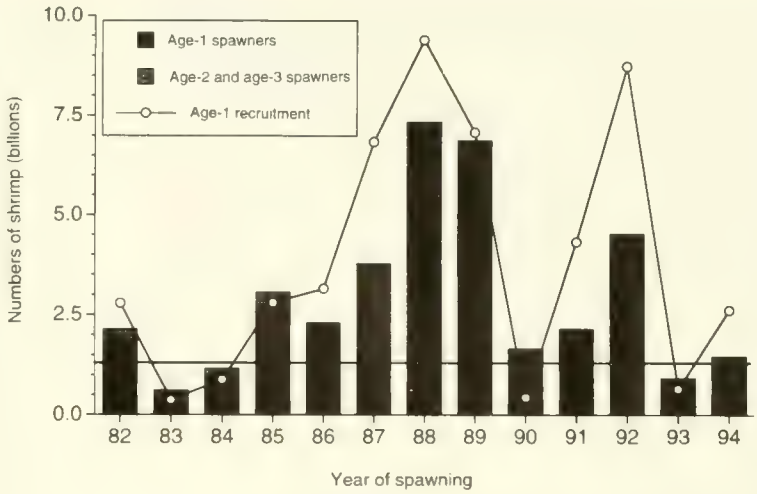

Figure 8

Ocean shrimp spawner index, broken down by age, and age-1 recruitment index for the same year, 1982–94. All data are calculated assuming elemental trawl efficiency of 0.50. Horizontal line indicates a hypothetical management threshold for spawner abundance.

Discussion

This analysis supports the hypothesis that the spring transition in coastal currents is important for successful ocean shrimp recruitment (Hannah, 1993). Although data from this effort and the prior study overlap for 10 of the 16 years presented here, new methods were used in this study that did not depend on constant catchability and were insensitive to failure in the assumption of constant natural mortality and insensitive to assumptions about trawl efficiency. The fact that this study and the earlier effort both found a strong correlation between recruitment and SLH in April of the year of larval release suggests that the interannual variation in shrimp recruitment is substantial, creating a strong "signal" that can be observed through considerable "noise" from various simplifying assumptions.

The precise mechanisms by which a large drop in spring sea levels coincides with strong recruitment of ocean shrimp remains a matter for speculation. This study did not attempt to investigate this issue. A more in-depth discussion of the alternative hypotheses can be found in the earlier paper (Hannah, 1993). The continued importance of April SLH as a strong correlate of shrimp recruitment suggests that further investigation of the potential mechanisms is warranted.

The principal novel finding of this study is the evidence for a stock-recruitment relationship for ocean shrimp. This evidence is statistical in nature and the data series is fairly short, suggesting that this finding should be considered preliminary at this time. The fact that much of the environmental variation in recruitment has been accounted for in the models, in combination with the lack of a serial autocorrelation in the recruitment index, supports the contention that an actual stock-recruitment relationship has been detected (Garcia, 1983). The form of the detected relationship corresponds to the ascending leg of the curve, indicating that some reduction in average recruitment has resulted from low spawner abundance. Unfortunately, the relationship demonstrated gives little indication of the shape of the right hand portion of the curve, leaving the proper functional form an open question.

With environmental variation strongly influencing ocean shrimp recruitment, the detection of a stock-recuitment relationship has different implications from those in a classical application of stock-recruitment theory. In stocks with reasonably stable recruitment, stock-recruitment curve parameters can, in theory, be used to determine a maximum sustainable yield. For shrimp, the multivariate recruitment models (Table 2) define a surface over which recruitment varies in response to the environment and changes in the level of spawning stock. The environmental influence on recruitment also implies a very strong recruitment-stock relationship; the points residing in the lower left corner of Figure 4 are not simply the result of fishing but are due to low recruitment in the parent years, in combination with fishing (Fig. 8). The main value of knowing that a stock-recruitment relationship exists for ocean shrimp is that it suggests strongly that there is a

level of fishing beyond which the average subsequent recruitment will be reduced. The distribution of stock and recruitment data in this study suggests that maintaining a "spawner threshold" for this stock unit should produce higher average recruitment (Fig. 4). The threshold suggested here, 1.3 billion spawning shrimp is, of course, not an absolute measure, but rather a level that is relevant only to the indices as constructed here, assuming elemental trawl efficiency of 0.50. If better information on the average elemental efficiency of shrimp trawl gear can be developed, then an actual spawning threshold can be calculated. With or without an absolute threshold, these data suggest that curtailing harvest in years of recruitment failure has the potential to increase subsequent average recruitment.

One seemingly surprising finding of this study is that egg production seems to offer little benefit over spawner abundance as an index of shrimp reproductive output. This result is partially an artifact caused by the two indices being based on the same underlying estimates of stock area and density, in combination with the use of a static length-fecundity relationship based on pooled data from several samples (Hannah et al., 1995). The egg production index incorporates only two additional sources of real variation: the variation found in the average size of females and in the percentage of females in the spawning population, and these parameters are not highly variable (Hannah et al., 1995). The finding that egg production estimates offer little benefit over estimates of spawner abdundance is also convenient because the flexible sex change exhibited by ocean shrimp makes it difficult to translate an egg production goal into a quantity that can be used to directly manage the fishery, such as a biomass threshold (Charnov et al., 1978; Hannah and Jones, 1991). To do so would require a way to accurately forecast the percentage of both primary females and age-2 males in the fall of the year, a technique not presently available.

The apparent influence of intense fishing on late egg-bearing females in April may have important implications for management of the ocean shrimp stock and suggests an important interaction between recruitment, parent reproductive output, and variation in the ocean environment. If the timing of the spring transition is indeed the critical determinant of ocean shrimp larval survival, then larvae released early and late in the spring may suffer very different fates, depending on when the spring transition occurs. When the transition is late, logic suggests that the magnitude of recruitment may depend very heavily on the survival of late release larvae, the very ones the fishery is capable of impacting heavily by harvesting egg-bearing shrimp. If this hypothesis is correct, it also suggests that environmental variation and the various measures of shrimp reproductive output one might use are confounded. For example, a large larval release in a year with a late transition may be the functional equivalent of a much smaller larval release in a year with an early transition; both result in low numbers of larvae released into favorable ocean conditions. Similarly, the impact on recruitment of harvesting late egg-bearing females could be large or minimal depending on the timing of the transition. For the 1989 year class, the impact was apparently quite severe, owing to a combination of a large catch of egg-bearing shrimp and a moderately high April sea level (Table 1), suggesting a late spring transition. The same amount of harvest may have had minimal impact on recruitment in a year with an early spring transition, when this hypothesis suggests that most of the larvae would have already been released into favorable conditions. Upon close examination, the interaction between variation in the timing of the spring transition and the timing and magnitude of larval release makes it unlikely that any simple measure of reproductive output would have direct explanatory power with regard to the level of subsequent recruitment. Such a mechanism could also be operating to obscure the stock-recruitment relationship in other stocks with an early critical stage and environmentally forced recruitment.

I consider the detection of a stock-recruitment relationship for this species to be a preliminary finding at this time. If this result endures as additional data become available, the implications for management of the ocean shrimp stock are still not entirely clear. Regulations aimed at eliminating, or severely reducing, the harvest of egg-bearing female shrimp in April may help increase average recruitment of ocean shrimp, with very little reduction in short-term yield. If the opening date of the ocean shrimp season were delayed 2–3 weeks, the harvest of egg-bearing shrimp in April would be virtually eliminated in areas 84 and 86 (Fig. 6). In more southern areas, like area 88, a full month delay is needed to eliminate harvest of egg-bearing shrimp (Fig. 6). With 6 months of fishing remaining in the open season, it is unlikely that annual exploitation rates would be greatly affected by a delay in the season opening date. Although major benefits from such a change in management would not accrue in most years, the evidence for a general stock-recruitment relationship suggests that some small increase in long-term average recruitment would result.

The other novel finding of this study concerns the strong recruitment-stock relationship for ocean shrimp, and its implications for managing highly variable, short-lived stocks. The data show that most

(2 of 3 observed) years of low spawner abundance result mainly from recruitment failures at age 1. This finding suggests that the classic management strategies, aimed at maintaining age-1 escapement rates, such as maximum count-per-pound and minimum codend mesh size, are unlikely to be very successful at reducing recruitment variability and increasing average recruitment for ocean shrimp. The reason for this is that by allowing increased escapement from an extremely depressed year class, there will be likely little impact on total spawner abundance. Rather, a strategy that reduces or eliminates exploitation of all age classes, once a year-class failure has been detected, has more potential to increase spawner abundance, simply because the remaining older shrimp may be more abundant than the failed age-1 year class. Another alternative, of course, is to manage at much lower exploitation rates, such that more shrimp survive to spawn at ages 2 and 3, although such a strategy is unlikely to maximize yield. The precise impact on yield of such an approach is difficult to predict without better knowledge of natural mortality rates. Natural mortality rates of ocean shrimp have been shown to vary widely, possibly in response to changes in the abundance of predator stocks (Hannah, 1995), such as Pacific whiting (*Merluccius productus*). Improved estimates of natural mortality rates for shrimp in turn depend on better knowledge of the elemental efficiency of shrimp trawl gear (Hannah, 1995). In addition, changes in management of this fishery should be geared towards maximizing economic rather than biomass yield (PFMC, 1981), suggesting that a comprehensive bioeconomic model is needed before the findings of this study can begin to be used.

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Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758)

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Abstract—The patterns of distribution and feeding habits of juvenile red porgy, *Pagrus pagrus*, were studied for fish collected in experimental trawl surveys carried out along the Cretan continental shelf over a period of four years. Abundance increased significantly in shallow waters, with a maximum between 20 and 50 m for all seasons, negatively correlated to depth and positively correlated to temperature. Patterns of bathymetric distribution were similar for all sizes of juvenile red porgy, varying little among seasons. The fact that no specimens larger than 219 mm FL were caught in the trawlable fishing grounds indicates that larger individuals aggregated over hardbottom areas that could not be sampled by trawling. Feeding intensity varied among the size classes of fish examined. Stomach-content analysis revealed that juvenile red porgy are carnivorous, feeding mainly on decapods. Diet composition did not vary seasonally; decapods were the most important prey throughout the year. However, the composition of the prey consumed varied considerably with predator size, coupled with differences in mean prey sizes found in each size class. Feeding rates of juveniles in terms of both feeding intensity and amount of food consumed were high and increased with fish size. The Cretan continental shelf habitat offers increased growth rate, reduced predation risk, and increased food abundance to juveniles and therefore they direct energy entirely into somatic growth. Juvenile red porgy appeared to be a separate unit, from a management as well as from an ecological point of view. Habitat segregation is of importance; juvenile specimens were differentiated from mature fish on the basis of their selection of bottom type and prey and to a lesser extent by depth.

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Spatial and temporal variation in population attributes, size and age structure, abundance and distribution, generally reflect life history properties of a species. Changes in diet or habitat (or both) during ontogeny are extremely common in fishes (Werner and Gilliam, 1984). Fish partition food resources between species as well as between size classes within a species. Similar mechanisms such as differences in morphological features, foraging behavior, period of activity and habitat use, affect segregation of resource use in both cases (Werner, 1979; Mittelbach, 1981; Ross, 1986; Norton, 1991). However, different ecological processes have been emphasized in interpreting the adaptive value of resource partitioning in these two situations. Partitioning among species has been argued to reduce interspecific competition (Sale, 1979; Osenberg et al., 1992; Schluter, 1994). By contrast, differential vulnerability to predators or the ability to exploit prey (or both) may lead to *de facto* partitioning of prey among age classes within a species, with the consequence that intraspecific competition is reduced (Werner et al., 1983). Many fish undergo ontogenetic changes in prey use between young-of-year and older stages. Both the ability to utilize the full spectrum of prey and to escape predators may be highly size related. Apart from changes in foraging demands, the vulnerability to predators decreases with increasing body size. Smaller fish frequently use sheltered habitats to reduce predation risk, whereas larger fish are often found in unprotected areas (Miller, 1979; Werner and Hall, 1988; McCormick, 1989). As a result of these changes in life style, fish may occupy different niches during ontogeny (Liem, 1984; Werner and Gilliam, 1984).

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a protogynous, sublittoral, demersal marine fish associated with a variety of temperate to subtropical habitats in the Atlantic and the Mediterranean Sea. It is commonly found on sandy, gravel, and hard bottoms, or around rocks, at depths ranging from 18 to 185 m (Manooch and Hassler, 1978; Vaughan et al., 1992). The correlation of age with maturity suggests that the majority of the females reach sexual maturity at three years (Manooch, 1976; Pajuelo and

Lorenzo, 1996; Harris and McGovern, 1997). The red porgy is of great commercial importance and consequently a highly exploited species in the areas of its distribution (Manooch and Hassler, 1978; Stergiou and Pollard, 1994). It is one of the most promising new species for fish farming in the Mediterranean Sea, having remarkably high growth rates under intensive rearing conditions. Therefore, the ambient demands of young individuals are of special interest for aquaculture (Divanach et al., 1993). The young individuals are distributed inshore of the adult population in trawlable areas. Even though they occur inshore as juveniles, adverse conditions of low water temperatures, competitive exclusion and unsuitable substrate reduce the longevity of this inshore distribution. Adult red porgy do not occur in the same shallow waters as those inhabited by juveniles. The larger fish predominate in deeper waters, preferring hard substrate (Manooch and Hassler, 1978). A general trend for larger fish to occur in deeper water has long been known with respect to deep sea fishes (Haedrich and Rowe, 1977); however it has also been mentioned by Macpherson and Duarte (1991) for many demersal fishes of the continental shelf. Caddy (1993) has stated that offshore movements of older fish to locations on untrawlable bottoms possibly contribute to the continuing good recruitment, as well as to the stock recovery.

Figure 1
Location of the sampling stations on the Cretan continental shelf.

The aim of the present study was to define the habitat use of juvenile red porgy along the Cretan continental shelf and to examine whether red porgy undergo considerable changes in resource utilization during ontogeny. In addition to determining bathymetric trends in mean size of red porgy, the relationship between density, depth, and temperature within size groups are defined. Furthermore, we investigated the effects of the feeding habits, prey choice, and trophic interactions among the different size groups on the distribution patterns of red porgy.

Material and methods

Study area and sampling procedure

A three-year survey on the distribution of red porgy was carried out along the Cretan continental shelf, from August 1988 to April 1991. Nine seasonal experimental bottom trawl survey cruises were conducted by the Institute of Marine Biology of Crete at 40 fixed sampling stations selected to cover all the trawlable fishing grounds of the region (Fig. 1). The collected data included abundance of fishes caught and supporting data on depth, temperature, and salinity. The cruise periods were as follows: late August to early September (summer), December (winter), and late March to early April (spring). The sampling stations were distributed over three distinct depth zones: 26–70 m (zone I), 71–150 m (zone II), and 151–350 m (zone III). Zone I covered 25%, zone II 24%, and zone III 51% of the total study area. Algae and marine angiosperms, mainly *Caulerpa prolifera*, *Posidonia oceanica*, and *Halophila stipulacea*, dominated the sand-silt substrate in zone I. The substrate of zone II was muddy and the substrate of zone III was covered by the crinoid *Leptometra phalangium*. Monthly samples (excepting January) from August 1990 to August 1992 were also taken from experimental trawl surveys in Iraklion Bay for stomach-content analysis. These samples were collected from a fixed station on the trawlable fishing ground of the region between 25 and 35 m during the morning, between 0830 and 0930 hours.

The trawl used was equipped with a codend bag liner of 22-mm stretched mesh size. The duration of each haul (bottom time) was 50–90 min and the trawling speed fluctuated from 1.8 to 3 knots, depending on the depth and nature of the bottom. Be-

cause all trawls were carried out with the RV *Philia*, it was assumed that gear selectivity was constant. Bottom temperature and salinity were measured with a SEA-BIRD CTD unit. The measurements recorded for the 5 m above the bottom of each station were averaged and the resulting values were considered as the temperature and salinity at the specific station.

Laboratory methods

Fork lengths (FL, mm) were measured for at least 100 individuals collected at each station and cruise. Of a total of 3280 fish, all specimens were found to be immature. To evaluate size-related variations in food habits and habitat use, red porgy were separated into five size classes: 0 (40–104 mm FL), 1 (105–147 mm FL), 2 (148–186 mm FL), 3 (187–219 mm FL), and 4 (>219 mm FL) which were chosen as they approximate the age of the fish within each size class as determined from the von Bertalanffy growth equation derived by Machias et al. (1998).

Each month 20–30 specimens were preserved in 10% buffered formalin immediately after capture for stomach-content analysis. Samples were taken to the laboratory, measured to the nearest mm (FL), and weighed to the nearest 0.1 g. Thereafter, the stomachs were removed and the contents wet weighed. Prey items were identified to the lowest possible taxonomic level, counted under a binocular microscope and weighed to the nearest 0.01 g. Prey species were measured to the nearest 0.1 mm by using an ocular micrometer or a vernier caliper, where possible. Fork length of the fish examined ranged from 41 to 185 mm, mean (±SD) FL was 87.2 (±26.9) mm.

Data analysis

In accordance with the procedure described by Carrothers (1980), the door spread of the trawl net was calculated for each haul and then multiplied by the speed of the boat and fishing time to estimate the total area sampled. The abundance of fish caught was expressed as number of individuals per square nautical mile (nmi^2), making the comparison of fish abundance between sampling stations possible. After logarithmic transformations (Middleton and Musick, 1986; Stefanescu et al., 1992), mean abundances (number/nmi^2) were calculated for each cruise: 1) for 20-m depth intervals, 2) for 50-m depth intervals, and 3) per zone (I, II, III), as well as for each 1°C temperature interval. Salinity showed little variation (Table 1), having no effect on the distribution of fishes on the Cretan shelf (Tsimenides et al., 1991).

Analysis of variance showed no significant differences in the mean abundance among the three surveys in each season, nor among each zone during the same season ($0.377<P<0.610$, Bartlet test $0.201<P<0.462$). Results and conclusions for each season were similar and independent of whether survey-specific or pool data were used. Hence, only the latter are presented. Correlation analyses (Pearson correlation coefficient) were performed to determine if there were any significant changes in abundance with depth and water temperature, as well as to test the hypothesis that fish size was depth or temperature dependent. Geometric mean was preferred for calculating the mean fish size of each sample, because the arithmetic mean is susceptible to the influence of few large specimens and does not accurately represent the central tendency in fish size at a given station (Stefanescu et al., 1992). The bathymetric distribution of different size fish was simplified by converting lengths into the above-mentioned five size classes.

The contribution of prey items to diet was estimated by using both the numerical abundance and the biomass of prey items in stomachs (Berg, 1979; Hyslop, 1980; Bowen, 1983). Breadth of diet was calculated by using Levin's standardized index (Hurlbert, 1978; Krebs, 1989):

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right),$$

where B_i = Levin's standardized index for predator i;
p_{ij} = proportion of diet of predator i that is made up of prey j; and
n = number of prey categories.

This index ranges from 0 to 1; low values indicated diets dominated by few prey items (specialist predators), higher values indicated generalist diets (Gibson and Ezzi, 1987; Krebs, 1989). Diet overlap between the size classes was calculated by using the simplified Morisita's index (Krebs, 1989; Hall et al., 1990):

$$C_{ik} = \frac{2\sum_j p_{ij} p_{kj}}{\sum_j p_{ij}^2 + \sum_j p_{kj}^2},$$

where C_{ik} = simplified Morisita's index for predators i and k; and
p_{ij} and p_{kj} = proportions of predator i and k with prey j in their stomachs.

Diet overlap increases as the Morisita's index increases from 0 to 1. Overlap is generally considered

to be biologically significant when the value exceeds 0.60 (Keast, 1978; MacPherson, 1981; Wallace, 1981; Langton, 1982). Bias-corrected bootstrap 95% confidence intervals, based on 1000 simulations, were used to estimate the reliability of these indices (Efron and Tibshirani, 1986; Hall et al., 1990). Differences in diet composition and stomach fullness by fish size and month were tested by χ^2 on combined data for both years because diet did not vary significantly between the two years. The logit model used to investigate monthly variations in the proportion of full and empty stomachs, as a function of fish size was

$$\log (p_d/p_d - 1) = a_d + b_d L + e$$

where p_d = the probability that a stomach is nonempty in month d;
L = the fish length; and
e = the error term.

One-way ANOVAs were used to compare the mean number, the mean weight, and the mean size of prey items among the size classes and the *a posteriori* Tukey's test was employed to locate the source of any differences. Numbers and weights of prey items were log-transformed to remove the dependency of the variance on the mean (Zar, 1984). Mean number and mean weight of prey per fish in each size class was based only on specimens with food items in their stomach. All statistical inferences were based on the 0.05 significance level.

Results

Distribution patterns

Red porgy were found to occur to 250 m depth, between temperatures of 14.5 and 24.2°C and salinities of 38.1 and 40.0‰ (Table 1). Abundance in the trawlable fishing grounds was negatively related to depth during all seasons and positively related to temperature during summer and winter (Table 2). No significant correlations between abundance and temperature were observed during spring.

The distribution of red porgy by depth intervals indicated that although fish generally occur in all zones, their abundance significantly increased in shallow waters (zone I), with highest values during summer (Fig. 2). Relative abundance was significantly higher in the shallow zone, with a maximum between 20 and 50 m depth for all seasons. Furthermore, the relative abundance increased progressively from winter to a maximum of 2985.6 individuals per nmi^2 in summer. These differences of the relative abundance in the shallow zone were mainly due to recruitment during summer.

Table 1

Seasonal ranges of depth and temperature over the Cretan shelf where *Pagrus pagrus* occurred.

	Minimum	Maximum	Range
Depth (m)			
Spring	30	110	80
Summer	28	210	182
Winter	29	250	221
Temperature (°C)			
Spring	14.5	17.3	2.8
Summer	14.5	24.2	9.7
Winter	15.0	17.8	2.8
Salinity (S‰)			
Spring	38.66	39.05	0.39
Summer	38.12	39.72	1.60
Winter	38.65	39.99	1.34

The relationships between mean FL and depth were significantly positive in summer and winter (Table 2). Maximum FL increases with depth only in summer, whereas the minimum and the mean FL increase during summer and winter. However, no significant correlation between FL and temperature was found (Table 2). Depth distribution by size revealed that fish larger than 186 mm do not occur in shallow waters, which were dominated by young fish (Fig. 3). Moreover, individuals larger than 147 mm were poorly represented at depths below 80 m. The abundance of the size classes 0–2 was greatest in warm waters during all seasons (Fig. 4).

Feeding intensity

Of the 634 stomachs of red porgy examined, 226 were found to be empty (35.7%). The proportion of empty stomachs varied significantly among the size classes of fish examined (χ^2=11.78, P<0.001), with a maximum of 39.6% for the 0 size class (Table 3). The logit model revealed that the interaction between month and fish size on the probability that a stomach is nonempty was significant (F=2.07, P<0.01). The slope was always >0, indicating a positive allometry on full stomachs, whereas no differences on the estimated probabilities were detected between the two years (t-test=–0.50, P>0.05).

Composition of the diet

There were at least 58 different prey species belonging to four major groups (decapods, small crusta-

Table 2

Correlation analysis between *Pagrus pagrus* abundance and fork length with depth and temperature. *r*: Pearson correlation coefficient, *P*: significant level of probability.

	Abundance		Mean fork length (mm)		Minimum fork length (mm)		Maximum fork length (mm)	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Depth (m)								
Spring	–0.524	0.03	0.084	0.79	0.207	0.52	0.217	0.50
Summer	–0.621	0.00	0.693	0.00	0.670	0.00	0.689	0.00
Winter	–0.598	0.00	0.701	0.00	0.685	0.01	0.167	0.58
Temperature (°C)								
Spring	0.224	0.10	0.633	0.07	0.070	0.85	0.585	0.10
Summer	0.787	0.00	0.401	0.25	0.510	0.13	0.621	0.06
Winter	0.349	0.01	0.138	0.74	0.097	0.82	0.299	0.47

Table 3

Feeding indices of *Pagrus pagrus* from the Cretan shelf, in relation to size.

Size class	Fork length (mm)	No. of stomachs analysed	No. of full stomachs	Mean no. of prey items per stomach[1]	Mean weight prey items (g) per stomach[1]	No. of prey species	Diet breadth (Levin's index)[2]	
							Number	Biomass
0	42–104	450	271	2.96[a] (± 0.23)	0.17[a] (± 0.01)	45	0.39 (0.22–0.50)	0.45 (0.31–0.56)
1	105–145	161	117	1.98[b] (± 0.20)	0.46[b] (± 0.01)	36	0.38 (0.22–0.50)	0.29 (0.15–0.38
2	146–185	23	20	2.23[b] (± 0.30)	0.77[c] (± 0.01)	27	0.373 (0.21–0.49)	0.20 (0.12–0.33)

[1] Standard error given in parentheses, different letters indicate significant differences among means (Tukey's test).
[2] Ranges in parentheses: 95% bootstrap confidence intervals

ceans, polychaetes, and fish) (Table 4). Polychaetes predominated in terms of percentage by number (35.1%), whereas decapods made up 54.2% of the total weight of stomach contents. Small crustaceans were also consumed in fairly large proportions by number (25.2%), but their contribution by weight was minor. Fish were a considerable dietary staple by weight (23.5%), although their contribution by number (6.7%) was comparatively low. At the species level, the thalassinid *Upogebia tipica*, the caprellid *Phtisica marina*, and the sedentary polychaete *Terebellides stroemi* were the most exploited prey. Among fish prey, *Gobius niger* was the species having greatest contribution in the diet of red porgy. Diet breadth was found to be 0.39 (±0.01) for the numerical abundance and 0.31 (±0.07) for the biomass of the prey species.

Food in relation to fish size

Although the contribution of prey groups, in terms of both number and weight, varied with fish size (Table 4), there were significant differences only between ingestion of small crustaceans (χ^2=28.46, P<0.001), *U. tipica* (χ^2=15.38, P<0.001), and *Liocarcinus maculatus* (χ^2=8.24, P<0.01). Small crustaceans occurred in the younger specimens (0 size class), whereas *U. tipica* and *L. maculatus* occurred in greater percentages in the diet of fish corresponding to size classes 1 and 2. The total amount of food ingested varied significantly among size classes (F=51.95, P<0.001). Pair-wise group comparisons showed three homogeneous groups: the mean consumption rate per individual (i.e. g food/size class)

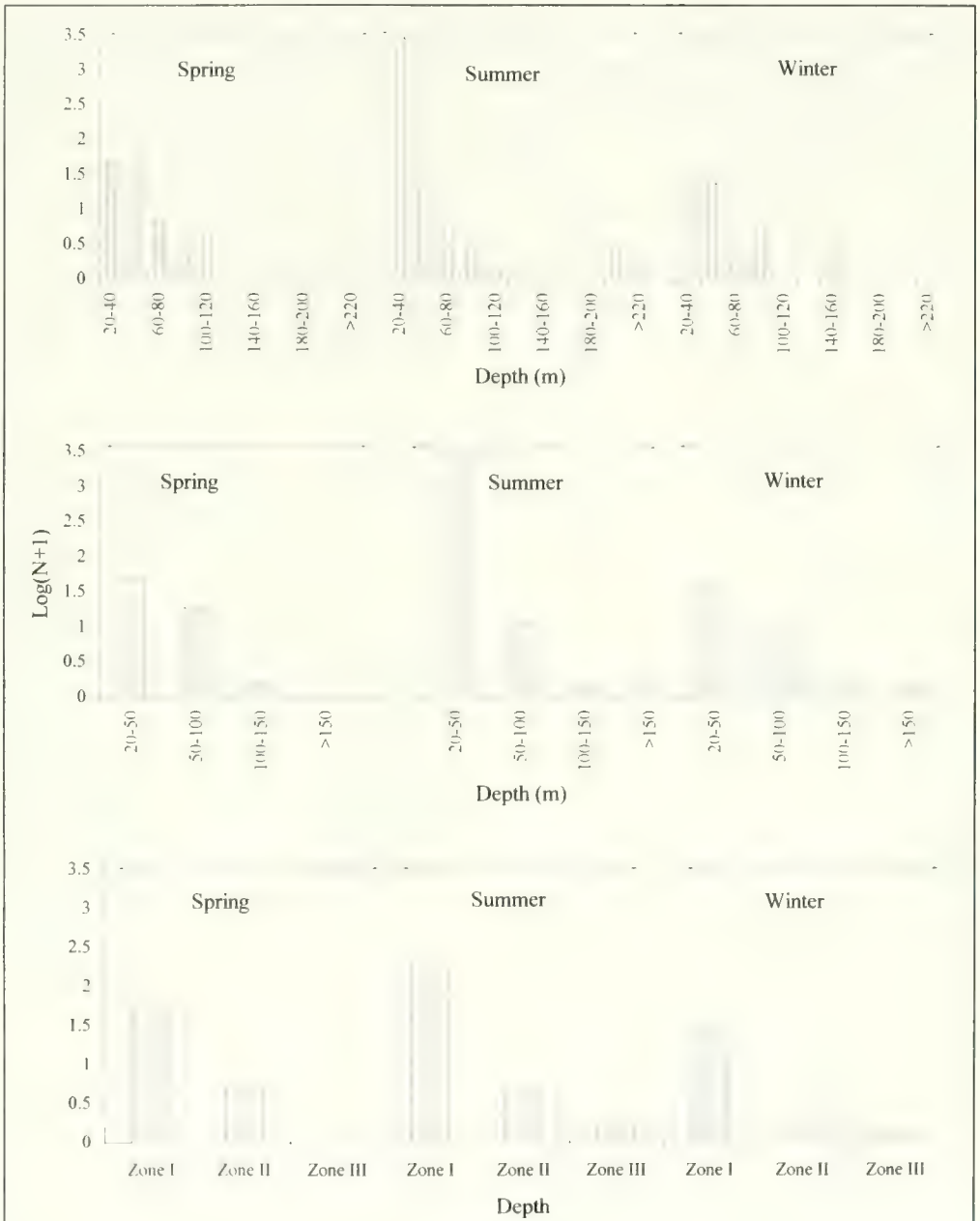

Figure 2

Seasonal distribution of *Pagrus pagrus* abundance in different depth ranges on the Cretan continental shelf. Log(N+1) = the average logarithm of the number of individuals per nmi^2.

increased with increasing size, with 0-size-class fish to exhibit the lowest consumption rate (Table 3). The mean number of prey items consumed decreased significantly with size (F=3.33, P<0.05) (Table 3).

Breadth of diet decreased with fish size, both numerically (abundance) and with biomass of prey species (Table 3). In general, values for dietary overlap between size classes were similar irrespective of the resource matrix used. A significantly high overlap was observed only between specimens of 1 and 2 size classes (Table 5).

Seasonal variation in diet

Diet composition was fairly consistent over the months (Fig. 5, A and B). Decapods were the most important prey throughout the year, especially during winter months and March, owing to the increase of the importance of the thalassinid *U. tipica*. Polychaetes were also an important component in the diet of red porgy throughout the year. Dietary breadth varied little, except for low values in winter months

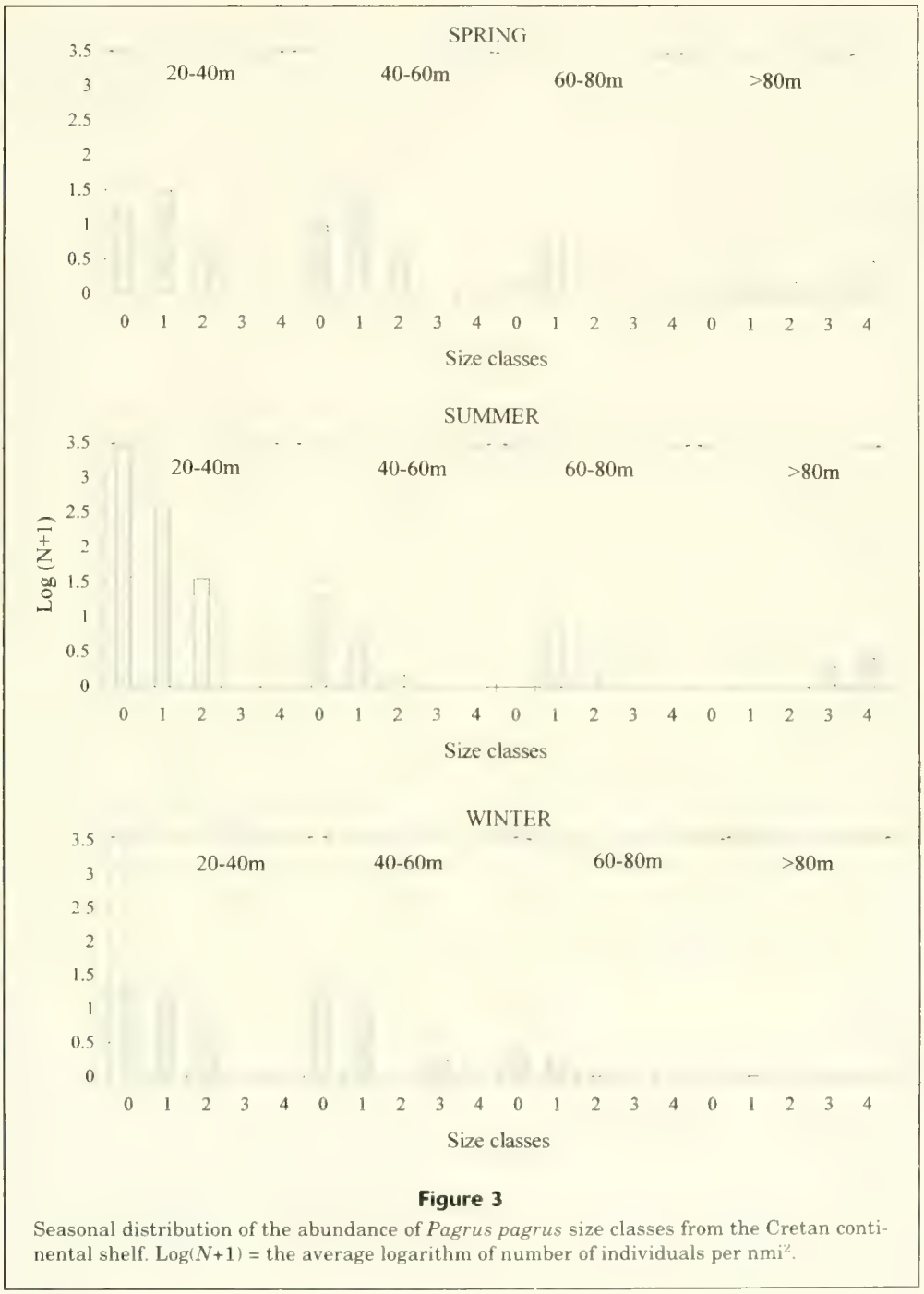

Figure 3

Seasonal distribution of the abundance of *Pagrus pagrus* size classes from the Cretan continental shelf. Log(N+1) = the average logarithm of number of individuals per nmi^2.

and March, when *U. tipica* dominated (Fig. 6, A and B).

Relationship of length of predator to length of prey

Significant positive correlations were found between the size of red porgy and the mean size of prey consumed (P<0.001, r^2=0.85, n=169). Furthermore, analysis of variance on the mean prey sizes consumed by the three size classes revealed significant differences (F=93.7, P<0.001). The 0-year fish exploited prey with smallest mean size (18 ±6.6 mm), 1-year fish consumed prey 26.2 ±5.4 mm, and 2-year fish fed on the largest prey (41.6 ±5.8 mm).

Discussion

Juvenile red porgy on the Cretan continental shelf tend to occur in shallows (20–50 m), where the sub-

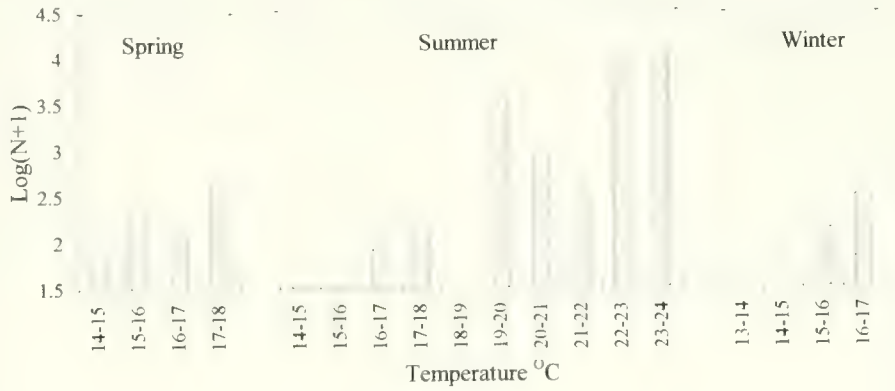

Figure 4

Seasonal distribution of *Pagrus pagrus* abudance in 1°C temperature intervals, on the Cretan continental shelf. Log(N+1) = the average logarithm of number of individuals per nmi^2.

strate is sandy and interspersed with patches of algae and seagrass. At this depth range, bottom water temperature is the highest during all seasons. Thus, this depth preference is consistent with the tendency for red porgy to select warm temperatures in relation to those available in other areas of its distribution (Manooch and Huntsman, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Although red porgy were found to occur down to 250 m depth, their densities were significantly greater at shallow stations. Furthermore, specimens smaller than 186 mm predominated in the trawl catches, whereas relative abundances of larger specimens was low. High densities of red porgy in shallow waters were due to the large number of juveniles, i.e. specimens that have not reached sexual maturity (Manooch and Hassler, 1978). The lack of larger fish from the trawl catches in shallower depths could not be due to gear selectivity because larger specimens were occasionally found in deeper waters, indicating that they could have also been caught in shallower depths, if present. A similar distribution pattern has also been reported for the Indo-Pacific species *Pagrus auratus* which has been studied in many different areas (Azeta et al., 1980; Kingett and Choat, 1981; Tanaka, 1985).

Size (or age) tends to be positively correlated with depth in many demersal fishes. Tremblay and Sinclair (1985) reported that the mean depth of occurrence tended to increase with age of cod in the southern Gulf of St. Lawrence. Similarly, Sinclair (1992) noted a positive correlation between age and median depth of cod on the eastern Scotian Shelf. Macpherson and Duarte (1991) found that mean fish length increased with depth in most south-east Atlantic and north-west Mediterranean demersal fishes. Bathymetric trends in demersal fish distribution may be linked to other physical factors correlated with depth (e.g. temperature, salinity, bottom type). Temperature is a key factor in the metabolism of fishes and many studies have reported relationships between temperature and fish distribution (Fry, 1971; Nakken and Raknes, 1987; Rose and Leggett, 1989; Macpherson and Duarte, 1991). However it is unlikely that fish distributions are determined by physical factors alone. Biotic factors, in particular prey abundance, have also been shown to be important determinants of distribution. Productivity generally decreases with increasing depth and distance from land; therefore prey resources are greater in shallow waters. Haedrich and Rowe (1977) concluded that selection for mobility and metabolic efficiency should favor larger size in the relative barren deep sea, whereas Macpherson and Duarte (1991) suggested that the positive size-depth relationship in demersal fish may result from age-specific differences in temperature preferences. They argued that younger fish occupy warmer waters, where food supply and growth rates may be greater, whereas older fish occupy colder waters, where they may benefit from lower metabolic costs and greater longevity.

The most striking aspect of our results, was the lack of variation in the bathymetric pattern of red porgy and the fact that depth distribution varied little among size classes, during all seasons. The scarcity of specimens larger than 187 mm in the bathymetric range >50 m is noteworthy, especially for a species with a life span more than 12 years (Vassilopoulou and Papaconstantinou, 1992). Thus the absence of mature specimens in trawl nets during the present

Table 4

Percentage contribution by number (n) and by weight (w) of the major prey taxa and species in the diet of each size class of *Pagrus pagrus* from the Cretan shelf. Prey occurring in >1% of the total are given. (+ = <1%; – indicates absence).

	n			w		
	Size classes			Size classes		
Prey category	0	1	2	0	1	2
Mysids	1.76	+	–	+	+	–
Polychaetes						
Terebellides stroemi	12.13	14.62	2.63	9.11	6.43	+
Aponuphis bilineata	7.35	9.67	–	5.22	2.57	–
Onuphidae	9.82	+	–	7.31	+	–
Glycera rouxii	+	11.12	4.13	+	4.22	1.03
Laetmonice hystrix	+	+	4.78	+	+	1.11
Other species	5.33	3.74	5.71	2.90	3.29	+
(Total polychaetes)	34.64	39.15	17.24	24.54	16.52	2.91
Small crustaceans						
Phtisica marina	20.95	+	–	+	+	–
Leptochelia savignyi	7.95	+	–	+	+	–
Apherusa chiereghinii	2.78	+		+	+	–
Other species	1.07	–		+	–	–
(Total small crustaceans)	32.75	+	–	+	+	–
Decapods						
Processa nouveli	2.14	+		2.47	+	–
Upogebia tipica	11.71	23.58	37.93	38.12	27.63	38.69
Paguridae	4.16	9.91	3.45	6.66	10.60	4.82
Ethusa mascarone	+	3.30	6.90	+	3.83	+
Liocarcinus sp.	+	2.83		+	4.00	–
Liocarcinus maculatus	1.76	6.13	24.14	2.49	5.74	26.13
Other species	2.14	+	–	3.11	+	–
(Total decapods)	21.91	46.69	72.42	52.85	52.20	70.15
Fish						
Gobius sp.	+	1.89	–	1.88	11.00	–
Gobius niger	+	4.25	6.90	5.34	9.22	23.52
Mullus barbatus		–	3.45	–	–	3.42
Other species	5.04	1.88		12.95	6.28	–
(Total fish)	5.79	8.02	10.35	19.47	26.50	26.94
Others	3.15	5.19	–	2.58	4.78	–

study almost certainly reflects aggregations of larger individuals on hard bottoms that were not trawlable. The maximum abundance of juveniles at 20–50 m could be related to the major availability of food resources at this depth range. Because nearshore areas typically contain a greater abundance of food (e.g. Hawkins et al. 1985; Swain, 1993) and a lower incidence of teleost predators (Werner and Gilliam, 1984; L' Abée-Lund et al., 1993; Ruiz et al., 1993), aggregations of young red porgy into shallow zone will result in an increase rate of growth and a lower mortality of these juveniles.

The composition of food suggests that the red porgy is a carnivorous species that relies on epibenthic invertebrates, mainly decapods. Despite the large number of taxa found in stomach contents, few species accounted for most of the prey consumed. The fact that the mean number of prey items per stomach was small (there was also a tendency for number of prey to decrease with fish size), indicates an active selection for prey taxa of large size. Moreover, specimens of each size class showed a further trend towards segregation of their feeding niches by consuming dif-

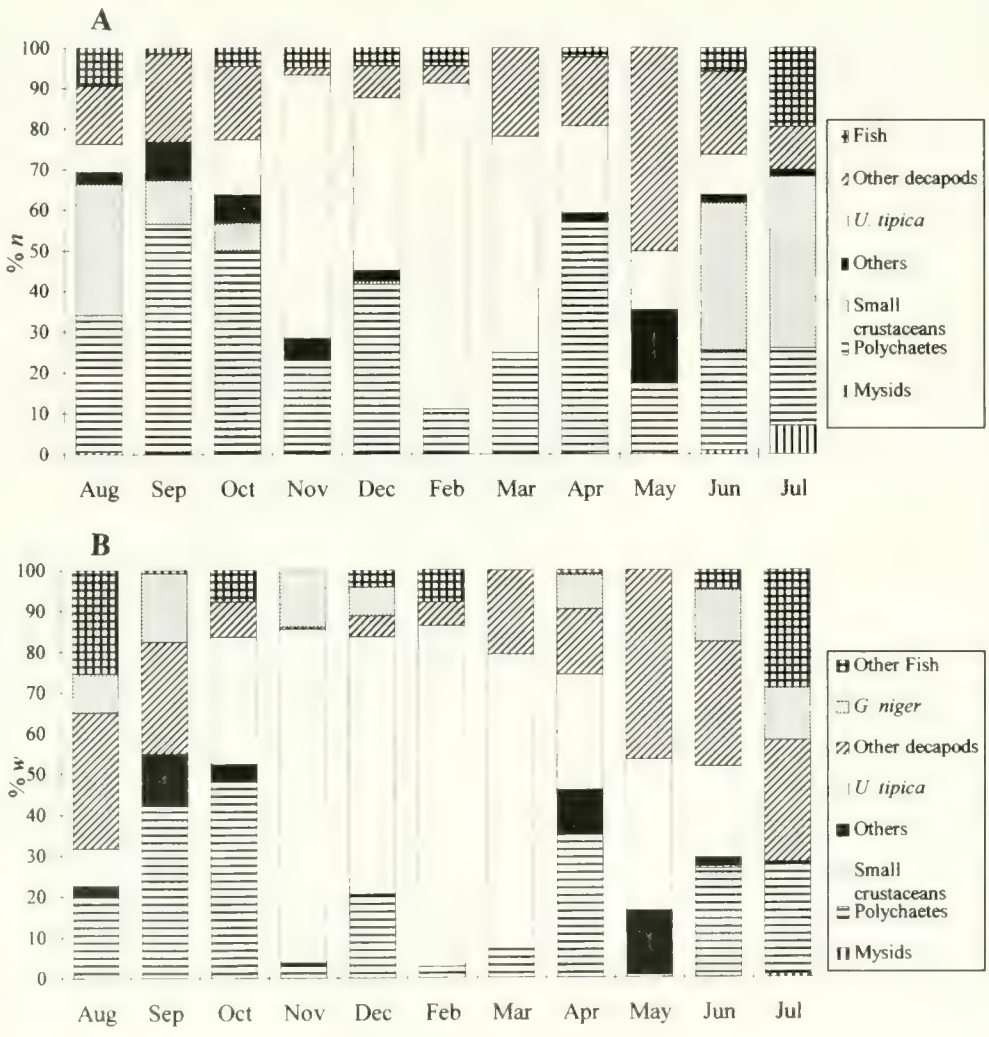

Figure 5

Monthly variations of the percentage contribution by number (**A**) and by weight (**B**) of the major prey groups and species in *Pagrus pagrus* diet.

ferent prey sizes. There is evidence that prey size differences reflect changing food preference with fish size, as well as the ability of larger individuals to capture larger animals. Mean prey-size increases with increasing predator size so that the energy return per unit of effort is optimal. The relatively high percentage of empty stomachs found in the 0 size class and the positive allometry on full stomachs suggest that feeding intensity increased with fish size. These results are not consistent with the general tendency of a decreased rate of metabolism typical of larger fish found in many studies (e.g. Smith and Page, 1969; Martin, 1970; Kislialioglu and Gibson, 1976; Fange and Grove, 1979; Werner, 1979; Grove and Crawford, 1980; Robb and Hislop, 1980), presumably because the specimens examined were immature. Hence it may be concluded that feeding rates exhibited by juveniles were high in terms of both feeding intensity and the amount of food consumed. Because red porgy on the Cretan shelf does not become mature until the third year of life, it remains for a long period in highly productive shallow waters and thus directs its effort entirely into somatic growth. The resultant increase in body size would thereby lead to an increase in the fecundity of individuals when they do, finally, become mature (Stearns, 1992).

Papaconstantinou and Caragitsou (1989) reported that in specimens >200 mm FL the importance of decapods, fish, and polychaetes declined rapidly with size, being replaced by anthozoans, brachyurans, and echinoderms. Unlike the results of the present study,

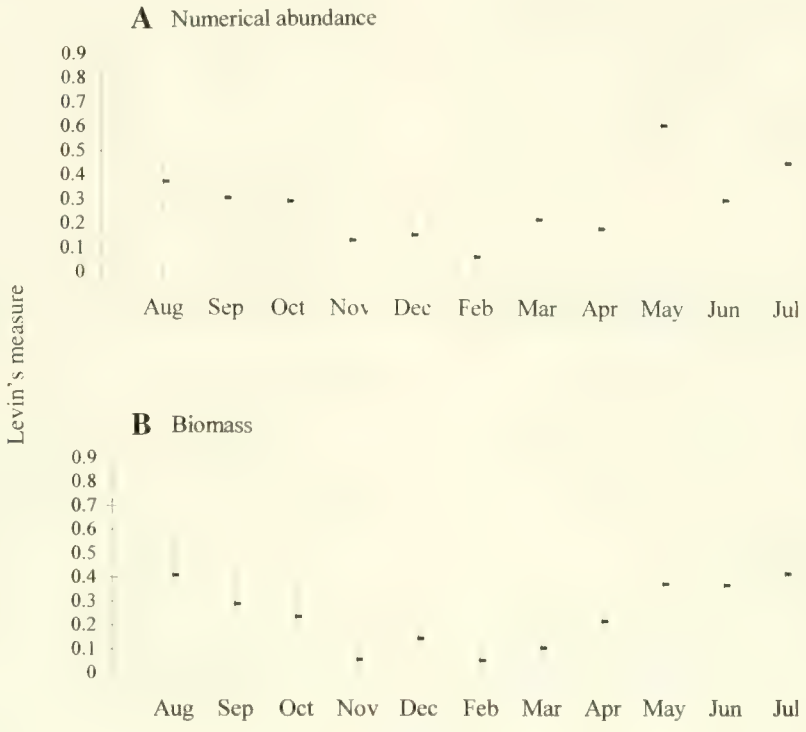

Figure 6

Monthly variations of *Pagrus pagrus* dietary breadth: numerical abundance (**A**); biomass (**B**). Error bars are 95% bootstrap confidence intervals.

their results showed pronounced seasonal changes in the diet of red porgy. It is possible that these differences in feeding habits between juvenile and mature individuals are associated with habitat change from soft bottom to hard substrates. Manooch (1977) stated that red porgy is an opportunistic browser feeding on a variety of invertebrates as well as small fish. He also noted that its diet appeared to be dependent on species availability, rather than preference or selection. These differences between our results and those of the previous studies may be due in part to the fact that in both studies dietary analysis was based on mature specimens, probably reflecting the distinct spatial zones occupied by juvenile and mature specimens.

According to our results, habitat of juvenile red porgy appears to be well separated from that of adult specimens. The absence of mature individuals in the trawlable fishing grounds indicates that recruitment in shallow waters is followed by an ontogenetic movement to a new habitat, at the time they reach sexual maturity. Further examination of this phenomenon is important from a biological, as well as from a management, point of view. Red porgy have previously been described as a food generalist obtaining most of its food from the benthos and epibenthos as well as a habitat generalist occupying a variety of habitats (Manooch, 1977; Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996). Patterns observed in the

Table 5

Diet overlap for the three size classes (0, 1, and 2) of *Pagrus pagrus* based on the numerical abundance and biomass of prey species. Ranges in parentheses: 95% bootstrap confidence intervals. Significantly high overlap values are in bold.

	Biomass	
Size class	0	1
1	0.44 (0.32–0.56)	
2	0.31 (0.18–0.48)	**0.73 (0.67–0.82)**
	Numerical abundance	
Size class	0	1
1	0.51 (0.31–0.66)	
2	0.36 (0.19–0.47)	**0.72 (0.57–0.84)**

present study suggest that habitat segregation is of importance; juvenile specimens are differentiated from mature ones on the basis of the bottom type and prey selection and to a lesser extent on the basis of depth.

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Nearshore hardbottom fishes of southeast Florida and effects of habitat burial caused by dredging

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Abstract.—Fish assemblages of nearshore hardbottom habitats of southeast Florida were quantified at three sites from April 1994 to June 1996. Random 2 × 15 m transects were visually censused within two replicate areas at each site. The hardbottom at one site was buried by a dredge project to widen a beach one year into the study. A total of 394 transects were sampled. Eighty-six taxa (77 identified to species) from 36 families were censused. Grunts (Haemulidae) were the most diverse family (11 species), followed by the wrasses (Labridae) and parrotfishes (Scaridae) with seven and six species, respectively. The most abundant species were sailors choice (*Haemulon parra*), silver porgy (*Diplodus argenteus*), and cocoa damselfish (*Stegastes variabilis*) with mean abundances (individuals/transect) of 4.5, 3.8, and 3.7, respectively. Early life stages (newly settled, early juvenile, and juvenile) represented over 80% of the individuals at all sites. Newly settled stages of over 20 species were observed in association with hardbottom reef structure. Outside of lagoons, nearshore hardbottom areas are the primary natural structures in shallow waters of mainland Florida's east coast and were estimated to have nursery value for 34 species of fishes. After one year, burial of approximately five ha of hardbottom habitat at one site lowered the numbers of individuals and species by over 30× and 10×, respectively. Due to their early ontogenetic stage, many of these species may not be adapted for high mobility in response to habitat burial. Dredging effects may be amplified by burial prior to and during spring and summer periods of peak larval recruitment.

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The southeast coast of mainland Florida is within a biogeographic transition zone of high marine biodiversity (Briggs, 1974; Gilmore, 1995). This region is also undergoing some of the most rapid human population growth of any area of the United States (Culliton et al., 1990). Due to the economic and recreational value of beaches, substantial marine dredging projects (up to 1.5×10^5 m^3 of fill/project) are commony used to widen beaches that are subject to erosion in the area (ACOE, 1996). Nearshore hardbottom habitats are the primary natural reef structures of this region at depths of 0–4 m and are often buried or indirectly affected by these projects. To date, no quantitative studies of the fish fauna of these habitats or the effects of beach dredge-and-fill projects on nearshore fishes are available (NRC, 1995).

Nearshore hardbottom habitats of this area are derived from accretionary ridges of coquina mollusks, sand, and shell marl which lithified parallel to ancient shorelines during Pleistocene interglacial periods (Duane and Meisburger, 1969; Hoffmeister, 1974). The habitat complexity of these limestone structures has been expanded by colonies of tube-building polychaete worms (Kirtley and Tanner, 1968) and other invertebrate and macroalgal species (Goldberg, 1973; Nelson, 1989; Nelson and Demetriades, 1992). In southeast Florida, most nearshore hardbottom structures are within 200 m of the shore. These habitats are often centrally located between mid shelf reefs to the east and estuarine habitats within inlets to the west. Therefore, they may serve as settlement habitats for immigrating larvae or as intermediate nursery habitats for juveniles emigrating out of inlets (Vare, 1991; Lindeman, 1997a). Nonetheless, most administrative reviews have concluded that the fish habitat value of nearshore hardbottom and the effects of dredge-based beach restoration projects are minimal (e.g. ACOE, 1996).

This study quantifies nearshore hardbottom fish assemblages on the southeast coast of mainland Florida over a 27-month period. The effects of dredge-fill placement were also examined because the hardbottom habitat at one site was buried on account of a beach restoration project 12 months into the study. Three primary objectives were examined. First, spatial and temporal attributes of fish assemblages at

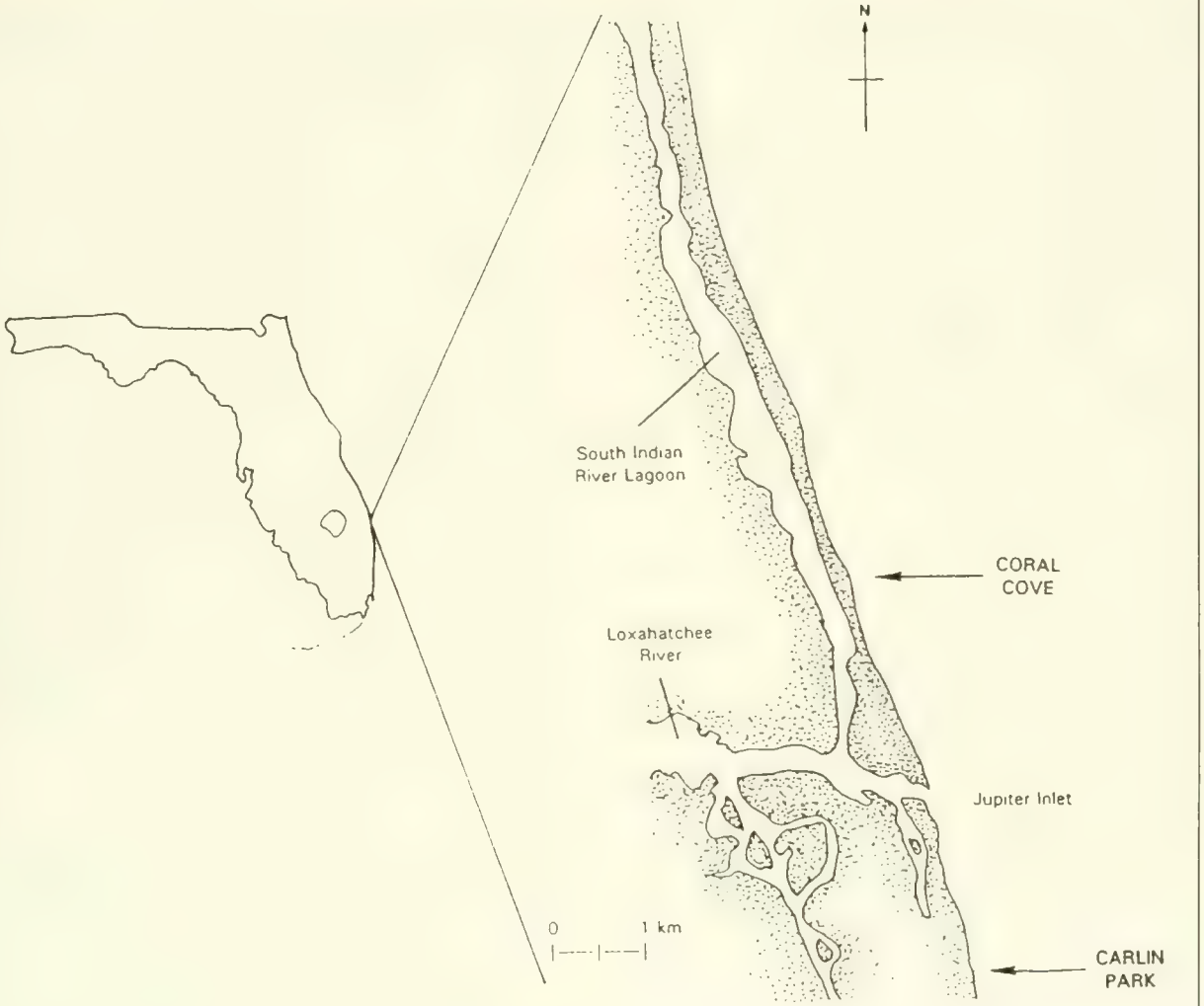

Figure 1

Primary study sites for fish surveys of nearshore hardbottom habitats at Jupiter, Florida (26°56'N, 80°04'W).

three undisturbed hardbottom sites were characterized. Second, abundances of different life stages were compared to assess the potential nursery value of nearshore hardbottom habitat. Third, effects of dredge burial on numbers of individuals and species were compared between a site subjected to burial and a control site.

Methods

Study areas

Fish abundances were quantitatively surveyed on two nearshore hardbottom sites approximately 2 km north (Coral Cove) and 2 km south (Carlin Park) of Jupiter Inlet, Florida (26°56'N, 80°04'W) from April 1994 through June 1996 (Fig. 1). Sampling at both sites extended approximately 100 m offshore to a depth of 4 m. Nearshore hardbottom of similar depth and structure at Ocean Ridge, immediately south of the South Lake Worth Inlet (26°31'N, 80°02'W) was also surveyed for comparative purposes during the summer of 1995.

Weathered limestone outcroppings were common between depths of 0 and 4 m at all sites. These structures have a variety of names (e.g. *Anastasia* formation outcroppings, coquina reefs, worm reefs) but are referred to by their most common name, "nearshore hardbottom," in the present study. In some areas, the hardbottom extended 1.75 m above the bottom and was highly convoluted. Shoreward portions of the hardbottom were exposed at low tide. Epibiota consisted of a variety of invertebrates and algae. The

most widespread encrusting organism was the reef-building sabellariid worm *Phragmatopoma lapidosa* (=*P. caudata*; Kirtley, 1994), often covering over 50% of the hardbottom at all sites.

A beach restoration project occurred at Carlin Park in March and April of 1995. More than 350,000 m^3 of beach-compatible sediments were excavated by a cutter-head dredge from a site 0.8 km offshore and hydraulically pumped along 1.8 km of shoreline. Bulldozers extended the fill seaward to an estimated width of 60 m. An estimated total of 4.9 to 5.7 ha (12–14 acres) of nearshore hardbottom was buried.[1] Visual surveys of fishes were conducted for 12 months before burial and 15 months after burial at both Carlin Park (the impact site) and Coral Cove (the control site). Little or no hardbottom was observed in fish surveys at Carlin Park after the project.

Survey protocol

During each site visit, three to five transects within two adjacent areas (=6–10 total transects/site) were censused. These 2 × 15 m transects were randomly located at depths ranging from one to four m. Transects were deployed along random compass headings at random distances between successive transects. Random number tables were used prior to site visits to determine the compass headings and distances between transects (based on numbers of fin kicks). All fishes observed within one m of each side of the transect line were identified and tallied by a snorkeler. The survey zone extended from the bottom to the surface and 2 m in front of the observer. Ledges and sand-rock interfaces were examined for fishes. Rocks were not overturned. The proportion of hardbottom to sand was estimated within each transect. An estimated 35% of the area within all transects was sand. Surveys were conducted between 0900 and 1700 and avoided twilight periods. To compare fish abundances at hardbottom and sand areas, identical transect methods were used at nearshore sand plains greater than 50 m from any hardbottom structures.

Monthly visual censusing occurred from April 1994 to June 1996 as permitted by nearshore visibility and sea state. Discharges of turbid water from Jupiter Inlet and wave resuspension of fine sediments sometimes resulted in turbidity levels that precluded sampling. Samples were obtained for all months except October through January when waves and turbidity were typically prohibitive.

[1] Davis, P. 1998. Palm Beach County Department of Environmental Resources Management, 3323 Belvedere Rd., Bldg. 502, W. Palm Beach, FL 33406. Personal commun.

In addition to total abundances, early life stages were also enumerated. Fork length was used for size estimation. Following Lindeman (1986; 1997a), life stages of grunts (*Haemulon* and *Anisotremus*) were recorded as follows: newly settled (<2 cm), early juvenile (2–5 cm), juvenile (5–15 cm), and adult (>15 cm). For other families, the same newly settled size range (<2 cm) was used. The early juvenile designation was used only for grunts because of the distinct morphological features of the 2–5 cm size range (Lindeman, 1986). Juvenile and adult stages were based on size and pigment patterns reported in the literature (e.g. Robins and Ray, 1986; Humann, 1994). Species identifications of the newly settled or juvenile stages for certain taxa were limited by very similar morphological features (e.g. scarids, kyphosids, gerreids, haemulids, clupeids). Some early stage identifications were therefore recorded only at the genus or family level. Collections of small schools of newly settled grunts were made with hand nets at both Jupiter sites in 1994 and 1995 to supplement field identifications. All collections were deposited at the Florida Museum of Natural History, University of Florida.

Data analyses

To address the first objective of our study, two complementary multivariate methods were used to spatially and temporally characterize the assemblages at the three sites. The second objective was addressed by univariate testing of the hypothesis that abundances of different life stages would not differ significantly within sites. The third objective was examined with the hypothesis that numbers of individuals and species would not differ significantly between an impact site where allmost all the hardbottom was buried and a control site that was unaffected by the burial. In univariate analyses, data were standardized as the mean number of individuals per transect and as the mean number of species per transect.

Samples were temporally unbalanced owing to the inability to visually sample during portions of the winter. Therefore, to examine the first objective, multivariate ordination and classification (cluster analysis) of a samples-by-taxa matrix for the entire, unpooled data set were used. These analyses were performed on a data set of 31 samples (16 from Coral Cove, 12 from Carlin Park, and 3 from Ocean Ridge) and 61 taxa. Each sample represented a site visit where 6 to 10 transects were censused. Samples from Carlin Park did not include postdredging site visits because these samples contained few or no fishes. The 61 taxa were those remaining from a total of 86 after eliminating taxa occurring only once across all

samples. Within each sample, counts for individual taxa were averaged over all transects to provide values for the matrix. These values were log-transformed [$\log_{10}(n+1)$] to prevent abundant taxa from dominating the ordination or classification results.

The transformed matrix was analyzed by correspondence analysis (CA), a method that employs a two-way weighted averaging algorithm to produce simultaneous ordination of sites and taxa (Gauch, 1982; Jongman et al., 1995). These analyses were performed with the program CANOCO (ter Braak, 1988). From the same log-transformed data matrix, normal (samples) and inverse (taxa) resemblance matrices were generated by using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Normal and inverse resemblance matrices were clustered separately by the unweighted paired-group method of averaging (UPGMA) (Sneath and Sokal, 1973). All dissimilarity and cluster analyses were computed with NTSYS-pc software (Rohlf, 1997).

To address the second project objective, numbers of life stages per transect were compared within each site. Data were analyzed by using a parametric one-way ANOVA when variances were homogeneous (Bartlett's test). *A posteriori* comparisons of differences among means employed Tukey's HSD test. Variances of numbers of life stages of grunts per transect at the two Jupiter sites remained heterogeneous after $\log_{10}(n+1)$ transformation and a Kruskall-Wallis non parametric, single classification ANOVA was used. Probability was calculated using the χ^2 approximation. Two-sample t-tests for unequal variances were used to compare numbers of individuals at hardbottom and natural sand sites. Only hardbottom samples from months when natural sand sites were sampled (March and April 1995) were used for these tests. In all statistical tests, differences were considered significant at $P<0.05$.

The third objective, examining dredging effects at the impact site (Carlin Park) and the control site (Coral Cove), employed a BACIPS (before after control impact paired series) design (Stewart-Oaten et al., 1986; Osenberg and Schmitt, 1996). This approach compares differences in variables between sites over time before and after the impact. The differences in the paired series were examined by two-sample t-tests by using the mean number of both individuals and species as the variables (Stewart-Oaten, 1996).

Results

A total of 352 transects was sampled at the two Jupiter sites: 204 at Carlin Park and 148 at Coral Cove.

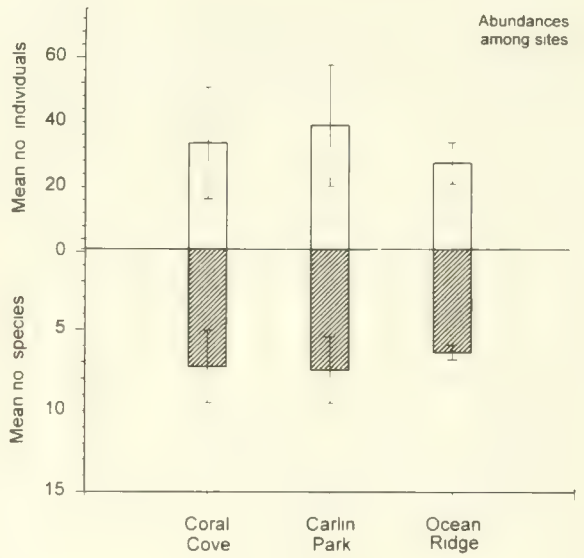

Figure 2

Mean number of individuals and species per transect (with 95% confidence intervals) for all nearshore hardbottom sites. Only predredging data were used for Carlin Park site. Sample sizes: Coral Cove: 148 transects; Carlin Park: 112; Ocean Ridge: 36.

At Carlin Park, 112 transects were sampled before burial and 92 after. At Coral Cove, 58 transects were sampled before the burial of the Carlin Park reef and 90 after. Eight transects were sampled over natural sand habitats at Carlin Park and six at Coral Cove. An additional 36 hardbottom and 6 sand transects were sampled at Ocean Ridge.

Family and species abundances

Thirty-six families of fishes were censused among the three hardbottom sites. The most speciose family was the grunts and margates (Haemulidae) with 11 species of *Haemulon* and *Anisotremus*. The wrasses, parrotfishes, and damselfishes (Labridae, Scaridae, and Pomacentridae) had seven, six, and five species, respectively. Four species each of jacks (Carangidae), snappers (Lutjanidae), and clinids (Labrisomidae) were recorded. These seven families contained 50% of the total species censused. Eighty-six taxa (77 identified to species) and 10,491 individuals were censused at all sites (Appendix). At Coral Cove, 64 species and 5093 individuals were recorded. At Carlin Park, 53 species and 4438 individuals were recorded. At Ocean Ridge, 48 species and 960 individuals were recorded. Mean numbers of both species and individuals per transect were similar among all sites (Fig. 2).

Table 1

Mean number of individuals/transect and frequency of occurrence for the most abundant three families, genera, and species at all nearshore hardbottom sites. Only predredging data were used for Carlin Park site. CC: Coral Cove (148 transects); CP: Carlin Park (112 transects); OR: Ocean Ridge (36 transects); GM: grand mean.

	Mean number/transect				% frequency occurrence			
	CC	CP	OR	GM	CC	CP	OR	GM
Family								
Haemulidae	15.5	17.4	9.4	15.5	89	90	92	90
Pomacentridae	5.9	7.9	5.7	6.6	81	95	86	87
Sparidae		5.9	3.7	3.9		37	44	38
Labridae	3.2			3.0	65			64
Genus								
Haemulon	9.8	15.3	6.2	11.4	75	80	42	75
Stegastes	3.4	6.1		4.3	72	89		73
Anisotremus	5.7		3.2	4.1	74		39	69
Diplodus		5.8	3.7	3.8		35	36	65
Species								
Haemulon parra	4.4	5.0	3.4	4.5	62	64	33	59
Diplodus argenteus		5.8	3.7	3.8		35	36	36
Stegastes variabilis		5.4		3.7		86		71
Labrisomus nuchipinnis	3.1			2.7	73			69
Abudefduf saxatilis			3.1	2.3	17			31
Anisotremus surinamensis	3.5			2.2			36	43

The three most abundant species were the sailors choice (*Haemulon parra*), silver porgy (*Diplodus argenteus*), and cocoa damselfish (*Stegastes variablis*) with means of 4.5, 3.8, and 3.7 individuals/transect over all sites (Table 1). The most abundant species at Coral Cove, sailors choice, black margate (*Anisotremus surinamensis*), and hairy blenny (*Labrisomus nuchipinnis*), represented 32% of all individuals. Seven of the 15 most abundant species at Coral Cove were grunts. At Carlin Park, silver porgy, cocoa damselfish, and sailors choice represented 41% of all individuals. Eight of the 16 most abundant species were grunts. At Ocean Ridge, the most abundant species were silver porgy, sergeant major (*Abudefduf saxatilis*), and sailors choice. Grunt species ranked first in frequency of occurrence per transect at Coral Cove and Ocean Ridge, and second at Carlin Park (Table 1). Damselfish species ranked first in frequency at Carlin Park and second at the other sites. The most frequently occurring species overall were cocoa damselfish, hairy blenny (*Labrisomus nuchipinnus*), and sailors choice (Table 1).

Normal cluster analysis of samples from all sites resolved three groups that broadly reflected temporal patterns (Fig. 3). No distinct spatial groupings emerged in the normal analysis. Group 1 consisted of 21 samples (eight from Carlin Park, ten from Coral Cove, and three from Ocean Ridge) mostly taken in spring and summer months. Group 2 consisted of 8 samples (four each from Carlin Park and Coral Cove) taken in mid and late summer. Group 3 included the only winter samples (February 1995 and 1996) taken during the project.

Inverse cluster analysis revealed seven groups of taxa (Fig. 4). Group A contained 26 common taxa including the most frequently occurring and abundant species from visual surveys such as sailors choice, cocoa damselfish, hairy blenny, and silver porgy (Table 1). This group characterized the spring-summer group of samples defined by normal group 1. The remaining six groups consisted of taxa that were temporally variable in their abundance and occurrence in the samples. Group B was characterized by species that occurred at lower abundances. Groups F and G were represented by single taxa: *Apogon maculatus* and *Archosargus probatocephalus*, respectively. The latter species was important in defining normal group 3 (Fig. 3).

Ordination of samples projected on CA axes 1 and 2 produced a pattern that generally agreed with the normal cluster analysis (Fig. 5A). The eigenvalue for CA axis 1 was 0.218 and accounted for 16.9% of the

variation in the data set, whereas the eigenvalue for CA axis 2 was 0.124 and accounted for 9.7% of the variation in the data set. Samples from August and September at Coral Cove and Carlin Park separated from all other samples along CA axis 1. In general, samples were not spread widely along CA axis 2; however, two samples, May 1995 at Ocean Ridge and February 1995 at Carlin Park, did separate from the other sites.

The ordination of taxa on CA axes 1 and 2 showed how the taxa were distributed in relation to the hardbottom samples along these same axes (Fig. 5B). The most common species (e.g. Table 1) clustered near the origin of the ordination. Taxa with high scores along CA axis 1 included infrequently occurring species such as *Halichoeres poeyi*, *Haemulon aurolineatum*, *Mulloidichthys martinicus*, and *Caranx ruber*. Low scores on CA axis 1 were *Echidna catenata*, *Acanthurus chirurgus*, *Chaetodon ocellatus*, and Sciaenidae sp. Species with high scores on axis 2 were *Sparisoma aurofrenatum*, *Chaetodon ocellatus*, and *Sparisoma viride*. These were most abundant at Ocean Ridge in May 1995 and were responsible for the separation of this sample from all others along CA axis 2.

In comparisons of hardbottom and natural sand, 20 transects over natural sand plains recorded only four taxa. The clupeid, *Harengula jaguana*, was most abundant (18 juveniles in two schools total). An unidentified *Eucinostomus* species, *Gerres cinereus*, and *Caranx bartholomaei* were also recorded (four, one, and one individuals, respectively). Hardbottom habitats typically had over thirty times the individuals per transect as natural sand habitats. Two-sample *t*-tests comparing hardbottom with sand habitats rejected the hypothesis of no differences in mean numbers of individuals per transect ($P<0.005$).

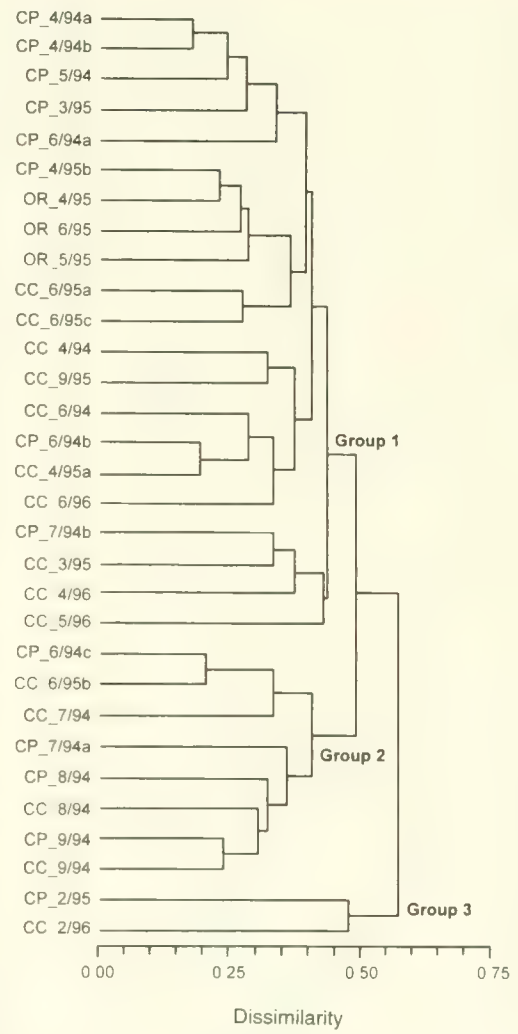

Figure 3

Clustering of visual census samples (sites and times) by UPGMA analysis of a normal Bray-Curtis dissimilarity matrix. CC: Coral Cove; CP: Carlin Park; OR: Ocean Ridge.

Life-stage abundances

At all sites, juveniles were the most abundant life stage among the top ten species (Table 2). At the two intensively sampled sites in Jupiter, the numbers of juveniles of all species pooled were significantly greater than any other life stage (ANOVA, $P<0.01$, Tukey's HSD). There were no significant differences in abundances among newly settled, early juvenile, and adult stages (Tukey's HSD). At both Jupiter sites, at least 80% of the individuals were early life stages (pooled newly settled, early juvenile, and juvenile stages)(Fig. 6). Abundances of newly settled and early juvenile stages at Ocean Ridge were similar to the Jupiter sites (Table 2), although numbers of juveniles and adults were lower. Newly settled stages of over 20 species were recorded on nearshore hardbottom structures among the three sites.

Eight of the ten most abundant taxa by site were represented primarily by early stages (Table 2). Cocoa damselfish and hairy blenny occurred most abundantly as adults. Adults of at least five of the top ten species occurred as residents, not transients. These included sergeant major, hairy blenny, cocoa damselfish, silver porgy, and black margate. Adults of a variety of less common species occurred but were often less abundant than early life history stages. Newly settled and juvenile stages often appeared to display more site-fidelity with hardbottom structure than did adults.

Six species of grunts (four *Haemulon* and two *Anisotremus*) and two species of damselfishes (*Stegastes*

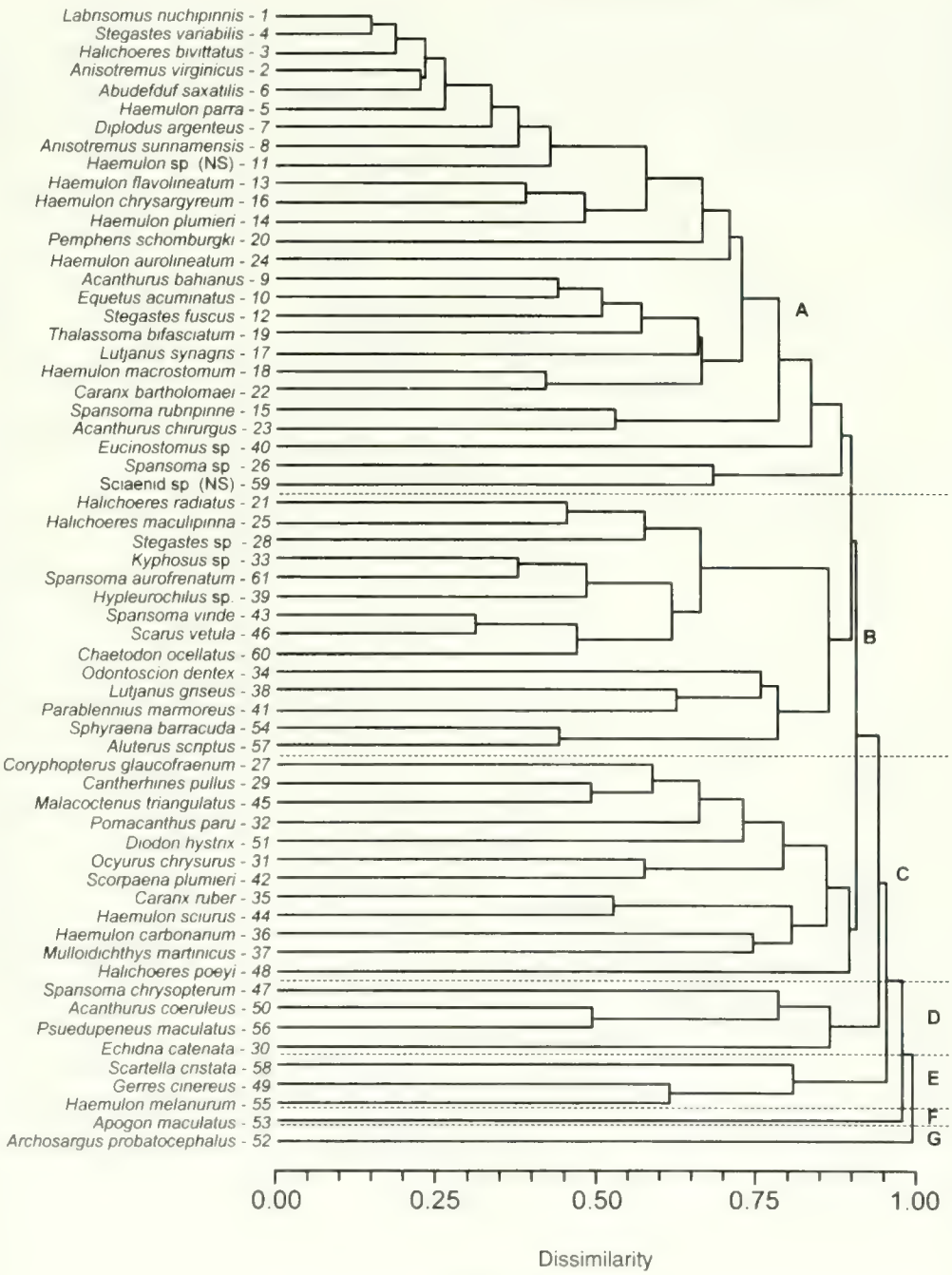

Figure 4

Clustering of fish taxa co-occurrence at three nearshore hardbottom sites by UPGMA analysis of an inverse Bray-Curtis dissimilarity matrix. Numeric codes used in correspondence analysis are next to each name. NS: Newly Settled. Dashed lines delineate groups A–G.

and *Abudefduf*) ranked within the ten most abundant species from all three sites (Table 2). Relative abundances of the life stages of all grunts censused at the Jupiter sites are shown in Figure 7. Early juvenile stages of the most abundant species, sailors choice, were significantly more abundant than any other life stage at each of the three sites (Kruskal-Wallis ANOVA, $P<.001$, and *a posteriori* pairwise comparisons). Adult sailors choice were significantly lower in abundance than juvenile stages (Kruskal-Wallis ANOVA, $P<0.001$). Black margate and porkfish, *Anisotremus virginicus*, ranked second and

Table 2

Mean number of individuals/transect by life stage for the ten most abundant taxa at each of three sites. NS: Newly Settled; EJ: Early Juvenile (for haemulids only); J: Juveniles; A: Adults. Only predredging data were used for Carlin Park site. na = not available.

	Mean number individuals/transect											
	Coral Cove 148 transects				Carlin Park 112 transects				Ocean Ridge 36 transects			
Species	NS	EJ	J	A	NS	EJ	J	A	NS	EJ	J	A
Haemulon parra	0.7	2.7	0.8	0.2	0.7	3.8	0.8	0.1	0.4	2.6	0.4	<0.1
Diplodus argenteus	0.3	na	1.7	0.3	1.6	na	4.1	0.1	0.7	na	2.8	0.2
Stegastes variabilis	0.2	na	1.4	1.3	0.4	na	1.4	3.5	0.4	na	0.9	0.6
Halichoeres bivittatus	0.2	na	2.3	0.5	0.3	na	2.1	0.5	0.3	na	1.1	<0.1
Labrisomus nuchipinnis	0	na	0.8	2.3	0	na	0.3	2.0	<0.1	na	0.5	1.8
Abudefduf saxatilis	0.4	na	2.0	0.1	0.3	na	1.1	0.4	1.3	na	1.7	0.1
Anisotremus surinamensis	0.4	1.9	1.1	0.1	0.1	0.3	0.3	0	0.5	0.6	0.4	0
Anisotremus virginicus	0.9	0.7	0.4	0.2	0.3	0.9	0.3	<0.1	0.9	0.2	0.4	0.3
Haemulon aurolineatum	0	0.7	1.0	0	0	0.1	2.5	0	0	0	0	0
Haemulon sp.	1.8	<0.1	0	0	2.1	<0.1	0	0	0.9	0	0	0
Haemulon flavolineatum	<0.1	0.6	0.3	<0.1	0	0.9	1.0	<0.1	0	1.1	0.1	0
Haemulon chrysargyreum	0	<0.1	0.3	0	<0.1	0.3	1.7	0	0	0	0	0
Total means of life stages per site	4.9	6.6	12	5.0	6.3	6.3	15.5	6.6	5 0	5.4	7.4	3.0

third in overall abundance among grunts and were represented by all life stages (Fig. 7). Tomtate, *Haemulon aurolineatum*, ranked fourth on the basis of large but infrequent influxes of early stages. Outside of these pulses, tomtate was not an abundant or frequently occurring species at any site during any life stage.

Some newly settled grunts could not be positively identified during visual surveys and were pooled as *Haemulon* sp. (newly settled larvae of *Anisotremus* are distinctive, Lindeman, 1997a). This group contained epibenthic larvae of several species and ranked tenth in abundance among all taxa (Table 2) and fifth among haemulids (Fig. 7). The largest component of these unidentified schools was probably sailors choice. This assumption is based on 1) the greater relative abundances of sailors choice early juveniles at all sites; 2) the close proximity of sailors choice early juveniles to these newly settled *Haemulon* sp.; and 3) collections of several newly settled *Haemulon* sp. schools most commonly contained sailors choice upon microscopic examination.

Early stages of commercially valuable species occurred infrequently during the surveys, although recreationally important species were common. The most abundant commercial family at the nearshore hardbottom sites was the Lutjanidae (snappers). Four snapper species, totaling 58 individuals, were recorded at all sites. Thirty-eight of these were lane snapper, *Lutjanus synagris*. Thirty-three of these were juveniles, the majority less than five cm. Five newly settled individuals (<2 cm) were also recorded. Ten yellowtail snapper, *Ocyurus chrysurus*, were recorded, nine small juveniles and one newly settled individual. Unlike grunts, newly settled and small juvenile snappers were not gregarious, occurring individually or in pairs near interfaces of hardbottom structure and sand. Gray snapper, *Lutjanus griseus*, and schoolmaster, *Lutjanus apodus*, occurred only as older juveniles or adults and in low numbers (eight and two individuals, respectively).

Comparisons of interannual and seasonal patterns of life stage abundances were limited by temporally unbalanced sampling. Wind and wave conditions from September through February made collection of nearshore visual data in fall and winter erratic or impossible. Several hurricanes during July and August of 1995 produced wave and turbidity conditions that interrupted summer sampling as well. Other phenomena, including high winds and discharges of turbid water from the Jupiter Inlet, also precluded sampling for extended intervals. Nonetheless, samples were obtained from Coral Cove (the control site) for three consecutive years for the months of April and June. Comparisons of both numbers of spe-

cies and numbers of individuals per transect for April among 1994–96 revealed no significant interannual differences (ANOVA, P=0.34; ANOVA, P=0.21). Identical comparisons for June among the same three-year period revealed no differences among mean numbers of individuals (ANOVA, P=0.06), but significant differences among numbers of species (ANOVA, P<0.05). Pairwise comparisons using Tukey's HSD showed that Coral Cove in June 1995 had significantly more species than in June 1996 (mean species numbers: 8.7 versus 5.3).

Seasonal occurrence of only newly settled stages was examined at Coral Cove (Fig. 8). The timing and abundance of species occurrences suggested seasonal variations with peaks of newly settled stages in late spring and early summer. Sizes and numbers of individuals typically increased as summer progressed. Abundances of early stages for most species appeared to be low in February and March prior to peak spawning activity for many species (García-Cagide et al., 1994). However, difficulties in the collection of visual surveys constrained the examination of fall and winter patterns.

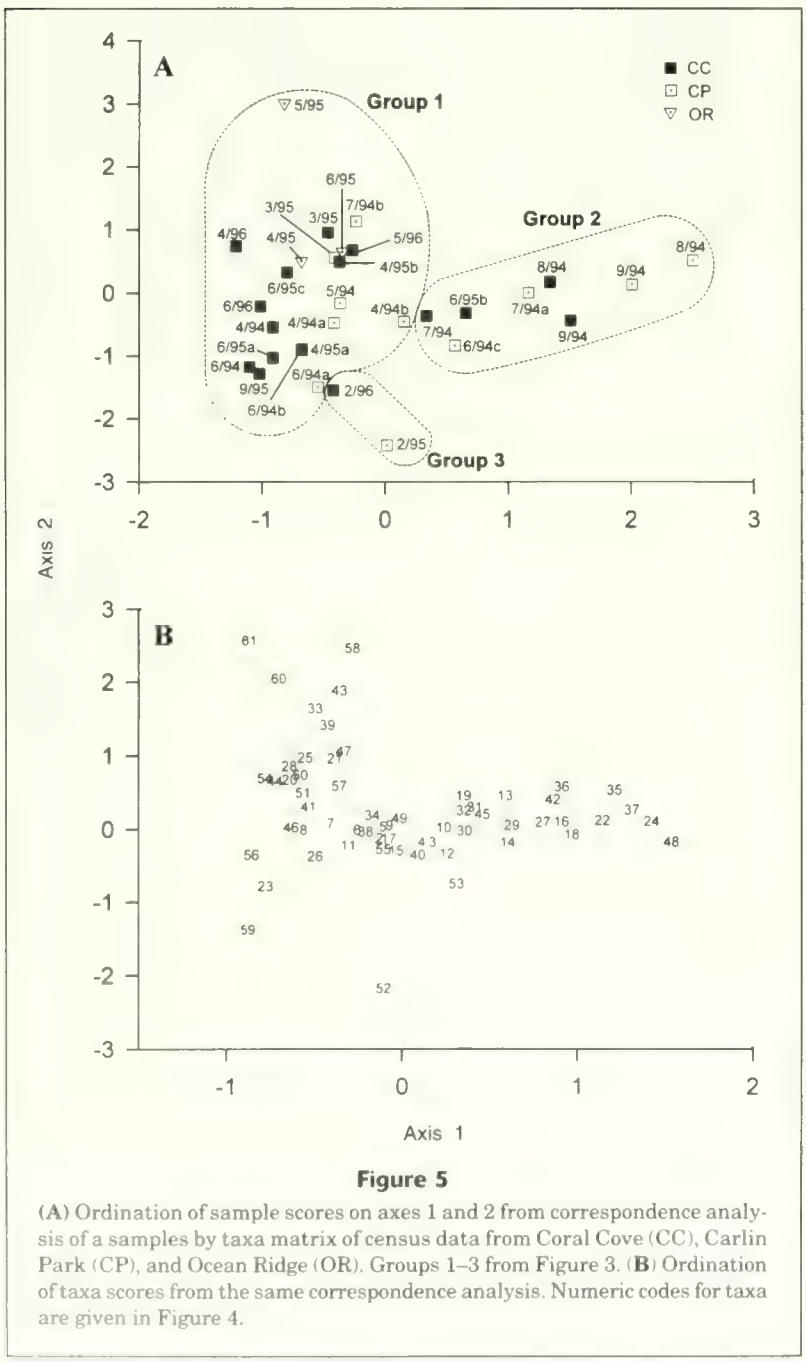

Figure 5

(**A**) Ordination of sample scores on axes 1 and 2 from correspondence analysis of a samples by taxa matrix of census data from Coral Cove (CC), Carlin Park (CP), and Ocean Ridge (OR). Groups 1–3 from Figure 3. (**B**) Ordination of taxa scores from the same correspondence analysis. Numeric codes for taxa are given in Figure 4.

Ichthyofaunal characteristics after habitat burial

Prior to habitat burial, fish assemblages at the two Jupiter sites were similar in species composition and relative abundance (Figs. 2, 3, and 5A). Pre- and postburial numbers of individuals and species at the control and impact sites are plotted in Figure 9. The hypotheses of no differences in total numbers of individuals and species before and after dredge burial of hardbottom were both rejected (P<0.001) in two sample t-tests for equal variances following a BACIPS design (Stewart-Oaten et al., 1986; Osenberg and Schmitt, 1996).

No fishes or exposed hardbottom were recorded in the first postdredging surveys at Carlin Park (13 April 1995). Several hardbottom outcroppings (1 m high by 3 m wide), parallel to the shore, were exposed at a depth of 1.5 to 2.5 m at the site during the second postdredging surveys on 24 April. Two of ten transects crossed narrow outcrops with dense schools of newly settled stages of three grunt species and one drum species (Sciaenidae). Before burial of the reef by extension of the beach width by approximately 60 m, such outcrops were deeper and further offshore than the original hardbottom sampling area. Small outcrops were still present in May and were occupied in two of ten transects by three species of grunts and one damselfish (Fig. 9). Schools of newly settled stages predominated. Such outcrops were not encountered during the 20 surveys in June, and no fishes were present with the exception of several round scad, *Decapterus punctatus*. Ten

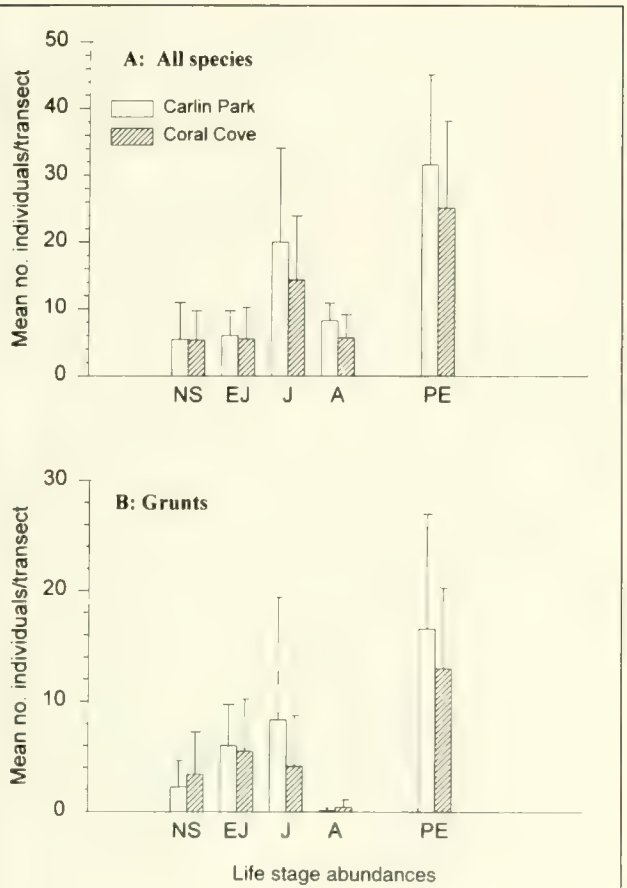

Figure 6

Abundances of different life history stages at the Jupiter hardbottom sites (with 95% confidence intervals). A: All species pooled. B: Pooled grunt species only. Only predredging data were used for Carlin Park site. NS: Newly Settled; EJ: Early Juvenile (for grunts only); J: Juveniles; A: Adults; PE: Pooled Early Stages (=NS+EJ+J).

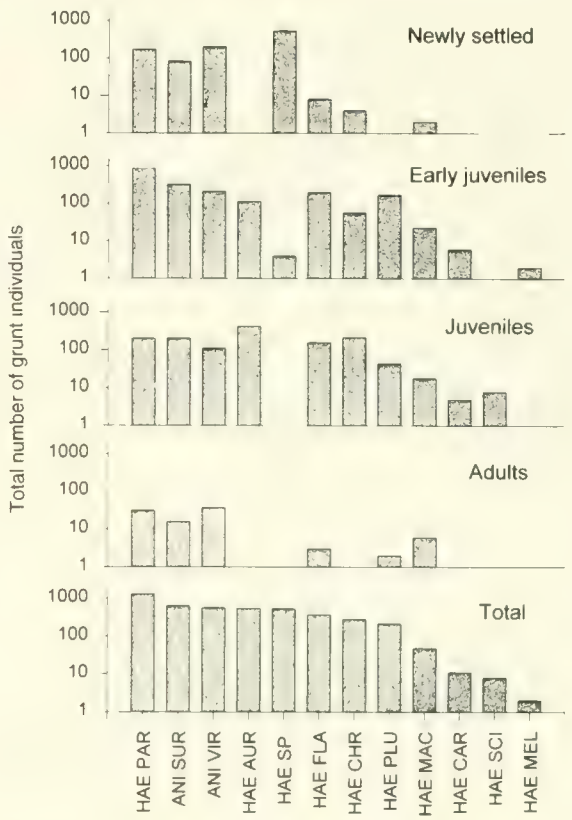

Figure 7

Comparative abundances of grunts among 12 taxa and 4 life history stages. Data pooled from all Coral Cove surveys and predredging Carlin Park surveys (260 transects total). Species represented by abbreviated genus and species names.

surveys in September 1995 recorded no exposed outcrops or fishes. During the following winter, erosion occurred and the width of the new beach was reduced. Some outcrops were re-exposed by the loss of dredgefill. However, wind and waves prohibited visual sampling during this period. Surveys in February, April, and May of 1996 (22 transects total) recorded no species (Fig. 9).

Discussion

Fish assemblages of nearshore hardbottom

The diversity of fishes utilizing nearshore hardbottom habitats of mainland Florida has not been quantified. Qualitative studies by ichthyologists experienced with the substantial taxonomic problems within these diverse, largely juvenile assemblages are also lacking. Three studies have included sections on nearshore hardbottom fishes as part of larger project goals. Gilmore (1977) listed 105 species in association with "surf zone reefs" at depths less than two m. Two additional species were added in later papers (Gilmore et al., 1983; Gilmore, 1992). Using visual surveys, Vare (1991) recorded 118 species from nearshore hardbottom sites in Palm Beach County. Futch and Dwinell (1977) included a list of 34 species obtained from several ichthyocide collections on "nearshore reefs." Including species from these prior studies, 192 species have now been recorded in association with nearshore hardbottom habitats of mainland southeast Florida (Table 3.3 in Lindeman, 1997a). Numbers of labrisomid, blenniid, gobiid, and apogonid species may be underestimated owing to their small size or cryptic behaviors. Other hardbottom habitats of the southeast United States occur in areas with substantially different physi-

ographic regimes (Sedberry and Van Dolah, 1984; Chiappone and Sullivan, 1994) and may show differing patterns of fish diversity.

Spatial and temporal attributes of fish assemblages at the three sites in the present study were examined by using ordination and cluster analysis. Visual census samples collected from March through July were similar in species composition and relative abundance among sites (Fig. 3). This finding is in agreement with the similar plots of individual and species abundances among sites (Fig. 2). The relative homogeneity of these samples was further reflected in the co-occurrence of many taxa including haemulids (*Haemulon parra*, *H. flavolineatum*, *H. chrysargyreum*, *Anisotremus virginicus*, *A. surinamensis*), pomacentrids (*Stegastes variabilis*, *Abudefduf saxatilis*), labrisomids (*Labrisomus nuchipinnis*), sparids (*Diplodus holbrooki*), labrids (*Halichoeres bivittatus*, *Thalassoma bifasciatum*) and scarids (*Sparisoma rubripinne*) (Fig. 4). With the exception of *L. nuchipinnis* and *S. variabilis*, most taxa occurred as early life stages.

Samples from late summer (August and September) were distinct from the spring and early summer in both cluster analysis and ordination (group 2, Figs. 3 and 5). The only two samples taken in winter (February) differed from all other samples in the analyses (group 3, Figs. 3 and 5). These patterns suggest that some seasonality in assemblage structure existed. This may reflect late spring and summer peaks in larval settlement in contrast to reduced winter settlement and, possibly, influxes of older juveniles from inshore lagoonal habitats. Substantial numbers of many species still settled in late summer but were possibly subject to higher predation from older individuals that settled earlier in the year. Various physical disturbances (e.g. winter cold fronts, summer hurricanes) and biological phenomena (variation in larval recruitment) affect the composition of fish assemblages of nearshore hardbottom. The turbidity generated by physical disturbances constrains the visual surveys needed to assess their immediate effects.

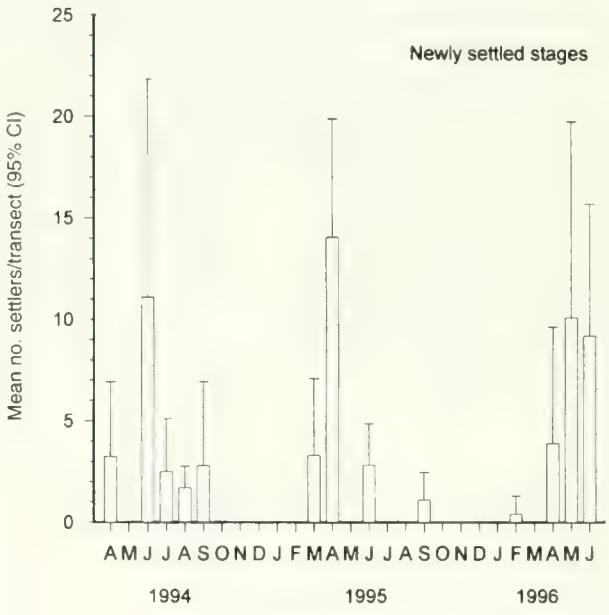

Figure 8

Mean number of newly settled individuals per transect for all species pooled at Coral Cove, 1994-1996 (n =148 transects).

Nursery habitats and nearshore hardbottom

With increasing human modifications of coastal areas, detailed knowledge of habitat usage is a key component of informed fishery and coastal land management. Identification of essential habitats includes the evaluation of spatial distributions of structural habitats across the shelf and habitat requirements of key taxa. Several lines of evidence suggest that nearshore hardbottom habitats along the mainland coast of east Florida can serve as nursery areas for many coastal fish species. Over 80% of the individuals at all sites were early life stages. Eight of the top ten species were consistently represented by early stages. Use of hardbottom habitats was recorded for newly settled stages of more than 20 species. In addition, other natural habitats with substantial vertical relief were absent from the shallow physiographic regimes where nearshore hardbottom occurred.

Although suggestive of nursery value, these lines of evidence need to be viewed in the appropriate context. High abundances of early life stages compared with adults do not guarantee that a habitat is a valuable nursery. High mortality rates in many reef fish populations (Sale, 1980; Shulman and Ogden, 1987; Richards and Lindeman, 1987; Jones, 1991) suggest that early stages will typically be more abundant than adults. If spatial distributions of all life stages are homogeneous, all habitats will have more early stages than adults. However, the abundances of early stages on nearshore reefs probably reflect more than just larger numbers of homogeneously distributed recruits. Newly settled stages of eight of twelve species of grunts and eight of nine species of snappers of the southeast mainland Florida shelf have been recorded primarily in depths less than ten m (Lindeman et al., 1998). Adults of most species are typically uncommon or absent in shallow habitats. There is considerable evidence for cross-shelf habitat seg-

regation among life stages of many grunt and snapper species from other regions as well; early demersal stages appear to most commonly use shallow habitats (Starck, 1970; Dennis, 1992). Similar ontogenetic differences in distribution and abundance exist for many other taxa that utilize nearshore hardbottom habitats.

Determining if the availability of habitat structure limits survival of early stages is important in assessing nursery value. Absences of habitat structure can result in increased predation or lowered growth (Hixon, 1991). In southeast mainland Florida, many natural nearshore marine habitats outside of coastal lagoons and between 25°30'N and 26°20'N (Dade and Broward Counties) are sand plains lacking hardbottom and substantial three-dimensional structure (ACOE, 1996). Although large stretches of nearshore hardbottom exist between 26°20'N and 27°50'N (Palm Beach, Martin, St. Lucie, and Indian River Counties) these habitats are often separated by kilometers of sand plains. There are no other natural habitats in the same nearshore areas that can support equivalent abundances of early life stages. These conditions could promote a demographic bottleneck that limits local adult populations owing to limited habitat availability for early stages.

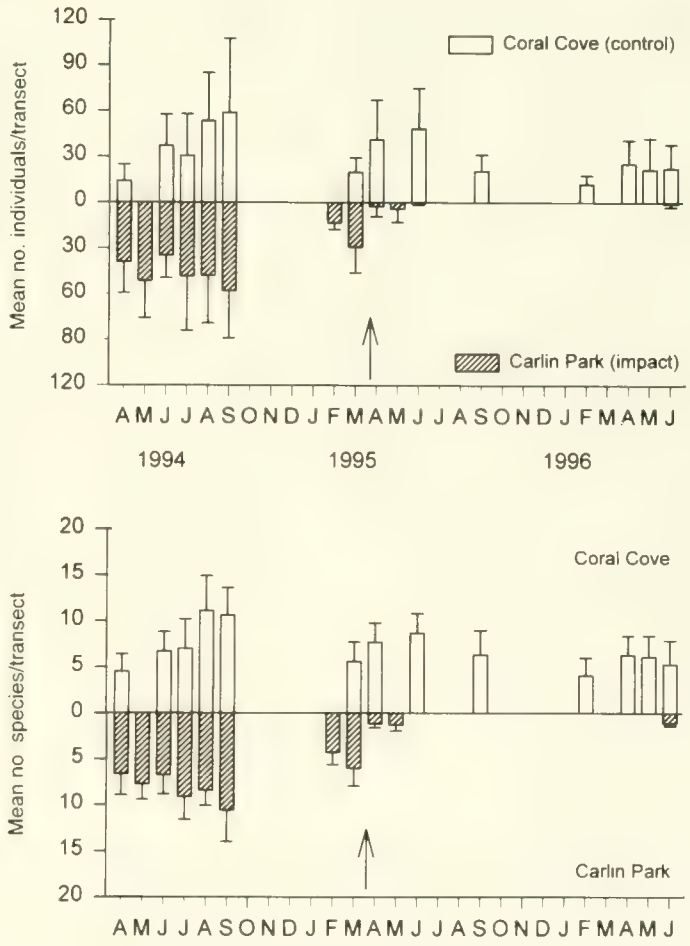

Figure 9

Mean numbers of individuals and species at control and impact sites in Jupiter, FL. Arrows indicate timing of dredge burial of hardbottom reef.

Despite their shallow depth, nearshore hardbottom reefs are positioned within current and tide regimes that can support considerable larval abundances. The occurrence of presettlement larvae in these areas is reflected by the abundances of newly settled stages in the present study and larvae in nearshore zones of Gulf of Mexico barrier islands (Ruple, 1984; Ross et al., 1987). Newly settled individuals were not recorded during any surveys of pure sand habitats in the present study. However, the presence of nearshore hardbottom promoted substantial colonization of shallow outcrops by larvae of many species, including haemulids, lutjanids, sparids, labrids, gerreids, sciaenids, and scarids. Ecotones with high vertical relief (e.g. hardbottom-sand interfaces near ledges) sometimes had large aggregations of newly settled stages of these taxa. However, microhabitat-scale distributions of fishes on nearshore hardbottom remain unquantified.

Use of nearshore hardbottom reefs as nurseries may be bidirectional across the shelf. Both inshore and offshore migrations during differing ontogenetic stages can be facilitated by habitats positioned centrally on the shelf. Nearshore hardbottom may serve a primary nursery role for incoming early life stages that would undergo increased predation mortality without shelter. Nearshore hardbottom may also serve as secondary nursery habitat for juveniles that emigrate out of inlets towards offshore reefs. This pattern is seen in gray snapper and bluestriped grunt which often settle inside inlets and primarily use nearshore hardbottom as older juveniles. In addition, some species use these structures as resident nurseries, settling, growing-out, and maturing sexually as permanent residents (e. g. pomacentrids, labrisomids). A secondary nursery role may also result from increased growth because of higher food availabilities in structure-rich environments. The intermediate cross-shelf positioning and other attributes reviewed above suggest nearshore hardbottom rep-

resents essential fish habitat for many species following NOAA (1996). Bidirectional use of nursery habitats positioned between inshore grassbeds and offshore reefs requires further study.

From abundance patterns of early life stages and the absence of any nearby natural habitats with high vertical relief, nearshore hardbottom of southeast mainland Florida was estimated to have nursery value for 34 species (Appendix). Empirical correlation of variation in early survival with adult population size is an important but rarely achieved component of nursery area evaluation. Combining experimental studies of habitat requirements with broad field surveys can aid in connecting organism-scale attributes with population-scale patterns (Serafy et al., 1997). Early demersal stages of several of the most representative taxa of nearshore hardbottom (e.g. grunt and damselfish species) can be collected and manipulated in the field and laboratory with relative ease (Lindeman, 1986; 1997a). These taxa may serve as useful models for nursery habitat studies that experimentally assess habitat requirements.

Effects of dredge-and-fill activities on ichthyofauna

Burial of the nearshore hardbottom habitat at Carlin Park with dredged sand significantly lowered the abundances of both species and individuals (Fig. 9). Before burial, 54 species were recorded, with mean abundances of 38 individuals and 7.2 species per transect (n=112 transects). After burial, eight species were recorded with mean abundances of less than one individual and species per transect (n=92 transects). No quantitative studies on the effects of nearshore hardbottom burial on fishes are available in the peer-reviewed literature for comparison.

The final supplemental environmental impact statement (EIS) for the Carlin project (Palm Beach Co. Dep. Environ. Resources Management, 1994) summarized several agency and contractor surveys between 1985 and 1990 at Carlin Park. Ten to forty-eight fish species were recorded from qualitative surveys of the hardbottom. Statements regarding the habitat value of nearshore reefs and dredging effects in the Carlin Park EIS emphasized the variable nature of reef exposure and forecast that fish impacts would be minimal and temporary. Primary impacts predicted for fishes were 1) short-term displacement during construction; and 2) temporary loss of food sources. The EIS also emphasized that impacts would be reduced by several features of the project design and nearshore environment. These features included the following: 1) the fishery value of impacted species was low; 2) some amount of hardbottom would remain or would be constructed for mitigation if needed; and 3) construction of the project would take place when fish populations were at their lowest. No mention of direct or indirect mortality upon fishes was made.

The biological assumptions within this EIS are similar to those found in related documents (e.g. ACOE, 1996). For the following reasons, it is suggested that some of these assumptions may be tenuous. The majority of individuals displaced by hardbottom burial in southeast Florida are early stages of economically and ecologically valuable species (Appendix; Figure 9). Early demersal life stages are particularly vulnerable to predators (e.g. Shulman and Ogden, 1987). Displacement was permanent for most individuals because almost all prior habitat was eliminated for at least 15 months (the postburial duration of the present study). Because of behavioral and morphological constraints on flight responses, high mortalities are probably unavoidable for many cryptic species, newly settled life stages, or other site-associated taxa subjected to direct habitat burial (Table 4.10 in Lindeman, 1997a). Whether a fish population is seasonally low at the time a project begins is insignificant if dredging will bury the habitat immediately before the peak period of larval settlement,[2] as in the Carlin Park project. In addition, loss of reef-associated food sources was probably substantial over this period.

No substantial habitat structure was present within at least 0.8 km of the Carlin Park reef during its burial. The closest natural structure was eastward at depths of at least 10 m. These deeper midshelf habitats may be utilized by relatively few grunt and snapper species during the newly settled and early juvenile stages. To the south, no substantial hardbottom was present for at least 4 km. To the north, the jetties of the Jupiter Inlet were approximately 2 km away. However, fishes in a northerly flight response had to negotiate a water column with zero visibility because dredge fill was dumped north-to-south. Any early stages of fish reaching the jetties would probably encounter high predation from older piscivores utilizing the large cavities among the armor-stone boulders of the artificially deepened jetty area (Lindeman, 1997a).

A postburial mitigation project using shallow artificial reefs of limestone boulders was proposed in the

[2] Hackney, C. T., M. H. Posey, and S. W. Ross. 1996. Summary and recommendations. *In* C. T. Hackney, M. H. Posey, S. W. Ross and A. R. Norris (eds.), A review and synthesis of data on surf zone fishes and invertebrates in the south Atlantic Bight and the potential impacts from beach renourishment, p. 108–111. Rep. to U. S. Army Corps of Engineers, Wilmington District, Wilmington, NC.

Carlin Park EIS. In the summer of 1998, three years after the burial, construction of approximately 1.6 ha of mitigation reefs began. If constructed before burial and at similar depths, mitigation reefs may have provided a refuge for a sizeable fraction of the thousands of displaced fishes during the burial of the hardbottom reef, as well as thousands of subsequent new recruits. Even with prompt construction of artificial reefs, many factors can limit the net production of biomass (Grossman et al., 1997). Some buried outcroppings were uncovered because of erosion of the project fill. However, structural support for two years of larval recruitment, shelter from postsettlement predation, and food for growth, were probably eliminated at the hardbottom burial site.

Nearshore hardbottom areas, such as Carlin Park, can be exposed to extended periods of wave energy and turbidity, particularly during winter months. However, conditions in winter do not dilute the potential significance of artificial burial during the spring and summer months. These are the periods of peak usage of hardbottom habitats by newly settled and juvenile stages of fishes. In the absence of dredging, nearshore areas typically show high reef exposures and reductions in physiological stressors during the spring-summer recruitment window. Elimination of this recruitment window by habitat burial for one or more years, regardless of winter dynamics, may substantially degrade the value of the primary natural nursery habitats along the windward shorelines of Florida's east coast. The above reasons suggest a risk-averse approach to hardbottom burial, as previously suggested for invertebrate fauna (Nelson, 1989).

The cumulative effects on fishes of repeated burial of nearshore habitats and other byproducts of these projects remain unknown. Cascading disturbances with ecosystem-scale effects can be hypothesized for a number of cumulative anthropogenic modifications in south Florida (e.g. Butler et al., 1995; Ault et al., 1998). Habitats affected by dredging or filling can show effects over temporal and spatial scales that are rarely considered (Vestal and Rieser, 1995; Lindeman, 1997b). For example, chronically elevated turbidities could lead to declines in primary production for frequently dredged areas of the southeast Florida shelf. Conclusive statements on the cumulative effects of large-scale dredging upon fishes will ultimately depend on the correlation of variations in early survival with adult population sizes, a rarely achieved task, even when effects may be substantial (Osenberg and Schmitt, 1996). However, the current absence of basic information on both short- and long-term scales can also be treated as an opportunity. Large dredge projects affecting midshelf and nearshore habitats will continue along the southeast Florida shelf at one- or two-year intervals. Basic questions on dredge-and-fill effects upon habitat use, predation, and growth, await study within a diverse assemblage of nearshore fishes.

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Appendix

Total abundances of all species visually surveyed at three nearshore hardbottom sites, southeast Florida. Only predredging data were used for Carlin Park site. * = hypothesized to use nearshore hardbottom as a nursery habitat (see discussion).

Rank	Common name	Species	Coral Cove	Carlin Park	Ocean Ridge	Total
1	Sailors choice	*Haemulon parra**	649	555	122	1326
2	Silver porgy	*Diplodus argenteus**	344	647	132	1123
3	Cocoa damselfish	*Stegastes variabilis**	420	600	66	1086
4	Slippery dick	*Halichoeres bivittatus**	439	327	50	816
5	Hairy blenny	*Labrisomus nuchipinnis**	463	262	81	806
6	Sergeant major	*Abudefduf saxatilis**	367	199	112	678
7	Black margate	*Anisotremus surinamensis**	513	68	55	636
8	Porkfish	*Anisotremus virginicus**	331	174	61	566
9	Tomtate	*Haemulon aurolineatum**	245	295	8	548
10	Grunt sp.	*Haemulon* sp.*	266	233	34	533
11	French grunt	*Haemulon flavolineatum**	134	210	43	387
12	Smallmouth grunt	*Haemulon chrysargyreum**	60	222	10	292
13	White grunt	*Haemulon plumieri**	70	150	1	221
14	Glassy sweeper	*Pempheris schomburgki**	153	21	32	206
15	Dusky damselfish	*Stegastes fuscus**	75	83	9	167
16	High-hat	*Equetus acuminatus**	54	59	13	126
17	Ocean surgeon	*Acanthurus bahianus**	51	12	17	80
18	Doctorfish	*Acanthurus chirurgus**	63	2	7	72
19	Redfin parrotfish	*Sparisoma rubripinne**	52	14	2	68
20	Mojarra sp.	*Eucinostomus* sp.	37	20	2	59
21	Spanish grunt	*Haemulon macrostomum**	14	35	1	50
21	Yellow jack	*Caranx bartholomaei*	9	41	0	50
23	Yellow goatfish	*Mulloidichthys martinicus*	34	8	0	42
24	Lane snapper	*Lutjanus synagris**	23	12	3	38
25	Bluehead wrasse	*Thalassoma bifasciatum*	22	7	7	36
25	Croaker sp.	Sciaenid sp.	22	14	0	36
27	Redtail parrotfish	*Sparisoma chrysopterum**	16	14	3	33
28	Damselfish sp.	*Stegastes* sp.	9	5	18	32
29	Parrotfish sp.	*Sparisoma* sp.	14	14	0	28
30	Reef croaker	*Odontoscion dentex**	13	3	8	24
30	Bar jack	*Caranx ruber*	2	20	2	24
32	Chub sp.	*Kyphosus* sp.	10	4	9	23
33	Bridled goby	*Coryphopterus glaucofraenum*	2	19	1	22
34	Clown wrasse	*Halichoeres maculipinna**	8	5	4	17
35	Anchovy sp.	Engraulid sp.	15	0	0	15
36	Puddingwife	*Halichoeres radiatus**	4	6	4	14
36	Orangespotted filefish	*Cantherhines pullus*	2	11	1	14
38	French angelfish	*Pomacanthus paru**	5	5	3	13
39	Seaweed blenny	*Parablennius marmoreus*	2	5	5	12
40	Caesar grunt	*Haemulon carbonarium**	3	7	1	11
41	Yellowtail snapper	*Ocyurus chrysurus**	3	5	2	10
41	Striped croaker	*Bairdiella sanctaeluciae**	10	0	0	10
43	Stoplight parrotfish	*Sparisoma viride*	4	1	4	9

continued

Appendix (continued)

Rank	Common name	Species	Coral Cove	Carlin Park	Ocean Ridge	Total
43	Redband parrotfish	*Sparisoma aurofrenatum*	1	0	8	9
44	Gray snapper	*Lutjanus griseus*	6	0	2	8
44	Porgy sp.	Sparid sp.	0	8	0	8
44	Bluestriped grunt	*Haemulon sciurus*	2	4	2	8
44	Spanish sardine	*Sardinella aurita*	8	0	0	8
49	Molly miller	*Scartella cristata*	2	5	0	7
49	Blackear wrasse	*Halichoeres poeyi*	6	1	0	7
51	Sheepshead	*Archosargus probatocephalus*	1	5	0	6
51	Blue tang	*Acanthurus coeruleus**	3	3	0	6
51	Spotted goatfish	*Pseudupeneus maculatus*	3	0	3	6
54	Saddled blenny	*Malacoctenus triangulatus**	1	3	1	5
55	Barbfish	*Scorpaena plumieri*	2	2	0	4
55	Queen parrotfish	*Scarus vetula*	0	1	3	4
57	Flamefish	*Apogon maculatus*	0	3	0	3
57	Yellowfin mojarra	*Gerres cinereus*	3	0	0	3
57	Blue runner	*Caranx crysos*	3	0	0	3
57	Spotfin butterflyfish	*Chaetodon ocellatus*	0	1	2	3
61	Balloonfish	*Diodon hystrix*	1	0	1	2
61	Chain moray	*Echidna catenata*	2	0	0	2
61	Scrawled cowfish	*Lactophrys quadricornis*	1	0	1	2
61	Schoolmaster	*Lutjanus apodus*	2	0	0	2
61	Blenny sp.	Bleniid sp.	2	0	0	2
61	Cottonwick	*Haemulon melanurum*	2	0	0	2
61	Great barracuda	*Sphyraena barracuda*	1	0	1	2
61	Scrawled filefish	*Aluterus scriptus*	1	0	1	2
69	Bicolor damselfish	*Stegastes partitus*	0	0	1	1
69	Orangespotted goby	*Nes longus*	0	1	0	1
69	Spanish hogfish	*Bodianus rufus*	0	1	0	1
69	Spotted snake eel	*Myrichthys acuminatus*	0	1	0	1
69	Gray angelfish	*Pomacanthus arcuatus**	1	0	0	1
69	Sharpnose puffer	*Canthigaster rostrata*	1	0	0	1
69	Greater soapfish	*Rypticus saponaceus*	1	0	0	1
69	Smooth trunkfish	*Lactophrys triqueter*	1	0	0	1
69	Hogfish	*Lachnolaimus maximus*	0	1	0	1
69	Puffcheck blenny	*Labrisomus bucciferus*	1	0	0	1
69	Nurse shark	*Ginglymostoma cirratum*	0	1	0	1
69	Squirrelfish	*Holocentrus rufus*	0	1	0	1
69	Blue angelfish	*Holacanthus bermudensis**	0	0	1	1
69	Rosy blenny	*Malacoctenus macropus*	0	1	0	1
69	Spotted moray	*Gymnothorax moringa*	1	0	0	1
69	Goldentail moray	*Muraena miliaris*	0	1	0	1
69	Atlantic spadefish	*Chaetodipterus faber*	1	0	0	1
69	Sand drum	*Umbrina coroides*	1	0	0	1
		Total taxa	72	60	50	86
		Total individuals	5093	4438	960	10491

Growth and maturation of the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991 (Crustacea, Decapoda, Callianassidae), a burrowing pest in penaeid shrimp culture ponds*

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Abstract.—Growth and sexual maturation were studied in the ghost shrimp *Lepidophthalmus sinuensis*, a pest species infesting oligohaline penaeid shrimp culture ponds on the Caribbean coast of Colombia. Sex ratio was significantly female-biased over four years of sampling. Development of ovaries, indexed as relative width, peaked prior to peak occurrence of ovigerous females and either coincided with or immediately followed the quarter of lowest ambient salinity. Ovigerous females occurred in all months, but the greatest mean percentage occurred in the first or second quarter of each year. Size and coloration of ovaries varied by maturational stage, and monthly counts of eggs per female peaked in February–April. Detection of recruits <8–10 mm carapace length (CL) was sporadic, and tracking of growth in recruitment cohorts was not possible. Mean CL of the population increased slowly over the first two years of sampling, as the percentage of males in the population increased. Sexual maturity in both males and females was evident in relative growth changes of the major chela. Analysis of growth in chela width, scaled to carapace length, suggested that males mature at about 11.0–11.3 mm CL, whereas females mature near 10.8–11.2 mm CL. Prematuration positive allometric growth did not differ between sexes, whereas postmaturation negative allometric growth in females differed significantly from strongly positive allometric growth in postmaturation males. Relative growth in wet weight of postmaturation males significantly exceeded that of postmaturation females. Expected female weight accumulations from episodic ovarian development were perhaps offset by simultaneous negative postmaturation growth of the female major chela. An understanding of growth, maturation, and the reproductive cycle of this shrimp species will help develop management strategies to control infestations by this callianassid pest species.

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In northern South America, the ghost shrimp *Lepidophthalmus sinuensis* Lemaitre and Rodrigues has been found restricted to oligohaline estuaries on the Caribbean coast of Colombia (Lemaitre and Rodrigues, 1991). From previous study of a congeneric species, osmoregulatory capacity and tolerance of hypoxia in this genus (Felder, 1978, 1979; Felder et al., 1986) appear to exceed abilities reported in most other callianassid genera (Thompson and Pritchard, 1969; Forbes, 1974, 1978; Mukai and Koike, 1984; Posey, 1987). Such adaptation has allowed members of the genus to exploit extensively low salinity habitats, especially richly organic silty bars and banks of lower river mouths or intertidal mudflats (Felder and Manning, 1997). In *L. sinuensis* and some eastern Pacific congeners (Nates and Felder, 1998), this adaptation also includes sediments of tropical, estuarine ponds in which penaeid shrimp are cultured.

Dense accumulations of ghost shrimp in these penaeid culture ponds are favored by their abbreviated larval development (Nates et al., 1997). At high levels of infestation by these burrowers, metabolic impacts and bioturbation appear to decrease penaeid shrimp production by reducing survival rates of postlarvae and slowing growth to marketable size (Nates and Felder, 1998). A thorough understanding of maturation and reproductive cycles in *L. sinuensis* is essential to devising effective long-term control measures for such infestations, especially to limit or replace the pesticide treatments that have been used to date (Nates and Felder, 1998). Thus far, timing and frequency of pesticide applications in shrimp mariculture have been devised by trial and error effects on penaeid production, without specific attempts to target treatments to peaks in reproductive activity of ghost shrimp or to achieve control by modifications in water management.

Although some species of the Callianassidae burrow to depths of 2 m or more (Pohl, 1946; Poore and Suchanek, 1988; Manning and Felder, 1991; Felder and Griffis, 1994), the difficulty of monitoring many natural populations has been overcome by collecting them with yabby pumps (see Manning, 1975). Several aspects of population biology for varied genera are now well documented (Pohl, 1946; Hailstone and Stephenson, 1961; Phillips,

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1971; Poore and Suchanek, 1988; Witbaard and Duineveld, 1989; Tamaki and Ingole, 1993; Rowden and Jones, 1994, 1995; Dumbauld et al., 1996), and the importance of callianassids in sediment turnover and nutrient cycling has been noted (Rowden and Jones, 1993; Ziebis et al., 1996). Ecological impacts of *Lepidophthalmus* spp. can dominate those of other estuarine infauna, as noted in recent studies of the warm-temperate species *L. louisianensis* in the northern Gulf of Mexico (Felder and Lovett, 1989; Felder and Griffis, 1994) and the tropical species *L. sinuensis* on the Caribbean coast of Colombia (Nates and Felder, 1998). Larval life histories for both *L. louisianensis* and *L. sinuensis* have been described (Nates et al., 1997), but later life stages and maturation remain little known for the tropical species *L. sinuensis*. Objectives of the present study were to analyze the periodicity and frequency of reproductive activity, to determine rates of growth in morphological features, and to define allometric indicators of maturation for populations of *L. sinuensis*. Resulting implications for management of penaeid shrimp ponds are discussed.

Materials and methods

All animals were obtained at the Agrosoledad S.A. shrimp farm on the upper Cispata estuary of the Río Sinú, Departamento de Cordoba, Colombia, near 9°17'N, 75°50'W. In order to avoid overt effects of pond harvesting, feeding, and other management activity, collections were restricted to bottom sediments of earthen drainage canals that extend for several kilometers through the farm. Specimens were individually extracted from burrows with yabby pumps (Manning, 1975), and samples included all animals retained when extracted sediments were washed on coarse (5-mm) sieves. All population samples were taken within 500 m of the upper end (origin) of the drainage canal system where colonized bottom muds ranged from about 3 to 6 m in width and population density ranged from 15 to 40 animals per m^2.

Monthly sampling of populations extended over four years from December 1991 through December 1995. Each monthly sample consisted of animals obtained from burrow openings encountered at random during walks along transects that crossed exposed mudflats at the sampling site during a period of reduced pond discharge. The sample consisted of at least 60 animals, and over 3200 animals were collected in the course of the study. Following collection, animals were transported in individual perforated vials (Felder, 1978) to the farm laboratory for morphological analysis. Specimens lacking chelipeds, having incompletely regenerated chelae, or with other obvious appendage deformities were excluded from the analyses that involved measures of those appendages but included in analyses of population size-class structure. In the laboratory, each individual was sexed on the basis of anterior pleopod morphological features and evidence of ovaries visible through the integument. Wet weight (WW) was determined to ±0.1 g on a top-loading balance after animals were blotted with tissue paper. Dry weight was estimated by drying the animals at 60°C for 48 h, and ash content was estimated from weight after ignition at 500°C for 6 h. When present, eggs on pleopods were included in weights of ovigerous females.

Morphometric measurements (Felder and Lovett, 1989) were made with dial calipers to ±0.05 mm. Because carapace length (CL) is usually less dependent on gonadal development than are most other size measurements (Hartnoll, 1982; Felder and Lovett, 1989), it was selected to represent body size and measured from the tip of the rostrum to the posterior margin of the cardiac region. Total length (TL) was measured from the tip of the rostrum to the posterior margin of the extended telson. Major chela height (ChH) was measured as the maximum height of the propodus, inferior margin to superior margin. Major chela width (ChW) was measured as the maximum width of the propodus from the most convex area on the internal surface to the opposite convex area on the external surface. Major chela length (ChL) was measured as the maximum length from the superior proximal articulation of the propodus with the carpus to the superior distal articulation with the dactylus. Between November 1992 and December 1995, ovarian width (OW) of females (the width of the right ovary visible dorsally through the integument of the third abdominal segment) was determined. An index of relative ovarian development was estimated from the ratio OW/CL. Color and number of eggs, color of the ovaries, evidence of parasites, and occurrence of damaged or missing chelae were also recorded. Egg size was measured under a light microscope and ocular micrometer. Volume of the eggs was calculated from the mean of the long and short axes used as the single diameter measurement for a sphere (McEdward and Chia, 1991).

Temperature and salinity were measured twice daily (dawn and dusk) at the surface and bottom of filled ponds. Temperature was measured ±1 °C with the probe of a YSI® model 57 temperature-compensated oxygen meter. Salinity ±1 ppt was measured with a temperature-compensated refractometer.

All means were reported along with the 95% CI (confidence interval). Monthly population samples were pooled to compare quarterly variations in the

distribution of size cohorts and the occurrence of ovigerous females in the population. Temporal trends in both carapace lengths and sex ratios for the overall four-year span of the study were analyzed by linear-linear piecewise polynomial regression to define slope transition points. Percentile data for the sex ratios were arcsine-transformed prior to these analyses. In order to remove effects of morphologically anomalous postreproductive and senescent individuals, animals >18.0mm CL (two females and three males) were excluded from analyses of relative growth. Linear-linear piecewise polynomial analysis of untransformed data was used to optimize positioning of ontogenetic transition points (±0.05 mm) in all relative growth comparisons. Except for this alternative method of iteratively locating slope transitions, methods complied with the recommended practice of fitting regressions to untransformed data above and below transition points by reduced major axis (Lovett and Felder, 1989). Standard allometric coefficients (Huxley, 1932) were also determined from regressions of log-transformed data by least squares estimate, with data subdivided at the previously estimated transition points. All statistical analyses were performed with NCSS® (Number Cruncher Statistical System) 6.0 software (Hintz, 1995).

Because generic revisions have yet to address many of the confamilial taxa that are treated in our comparative discussions, it was necessary in comparative discussions to refer to some species under *Callianassa sensu lato* (s.l.), while acknowledging that *Callianassa sensu stricto* has been restricted to a few eastern Atlantic populations (see Manning and Felder, 1991).

Results

Sex ratio

Except for January to June 1992, March 1993, and February 1995, sex ratios were significantly female-biased over the four years of sampling (Fig. 1A). Over the entire study period, the mean sex ratio was 2.4 ±0.3 females per male, with the lowest mean ratio (1.1) occurring in February 1992, and the highest ratio (5.1) in October 1993. Trends in mean CL of the population (Fig. 1B) generally tracked those in sex ratios, as defined by piecewise regression analysis. Slopes over the first two years revealed declining relative abundance and increasing mean CL of males, patterns that differed significantly from those of the last two years of monitoring. An iteratively optimized transition point for sex ratios occurred at 23 months, whereafter mean sex ratios remained near asymptotic. Analysis over the full study period also defined an optimized transition point or peak in CL of males at 23 months, beyond which male CL was asymptotic. The CL of females, however, peaked late in the first year of monitoring.

Mean size of both males and females increased slightly but significantly from the first through fourth quarter of each year except for 1994, a year in which the presence of first quarter recruits was offset by a cohort of large individuals surviving from the previous year (Fig. 2). When treated separately, mature-sized individuals (>11 mm CL) of both male and female populations increased in mean CL over the year, usually peaking in the fourth quarter prior to maximum abundance of ovigerous females in the following year (Fig. 3, B and D). Mean CL of males appeared to exceed slightly that of females over the full study period, and males dominated large size classes (Figs. 1B, 2, 3B). Only 4.3% of the collected females were >15.0 mm CL, whereas 12.4% of males attained this size. The largest animal collected was a 20.7-mm-CL male. Detection of recruits <8–10 mm CL was sporadic throughout the study (Fig. 3E), and tracking of growth in recruitment cohorts was not possible.

Ovigerous females

Among all ovigerous females collected during the study (n=444), size ranged from 7.04 mm CL to 16.8 mm CL. However, 38.3% of all these were in the 13.0 to 13.9 mm CL size class and <1.5% of ovigerous females were <11.0 mm CL (Fig. 4). The single ovigerous specimen <9.8 mm CL was an apparently precocious individual taken in August 1994, while the population of ovigerous females was low (Fig. 3D). During peak abundances of ovigerous females (February to June, Fig. 5B), 64.3% of females in the 13.0 to 13.9 mm CL size class were ovigerous (Fig. 2).

Ovigerous females were found in all months of the four-year study (Figs. 2 and 3D). However, percentages were lowest in the third quarters of 1992, 1993, and 1995, and the fourth quarter of 1994, whereas the highest percentages occurred in the first or second quarter of each year. Peak abundance of ovigerous females coincided with the highest quarterly salinity in 1992, 1994, and 1995 but was less defined in 1993 when the fourth quarter salinity did not fall to a typical low value (Fig. 3, A and D). When monthly samples were pooled over the entire study, highest percentages of ovigerous individuals among all females were evident during the high salinity period from February to June; a maximum was found in May (35.7%), three months after peak development of the ovaries (Fig. 5, A–C).

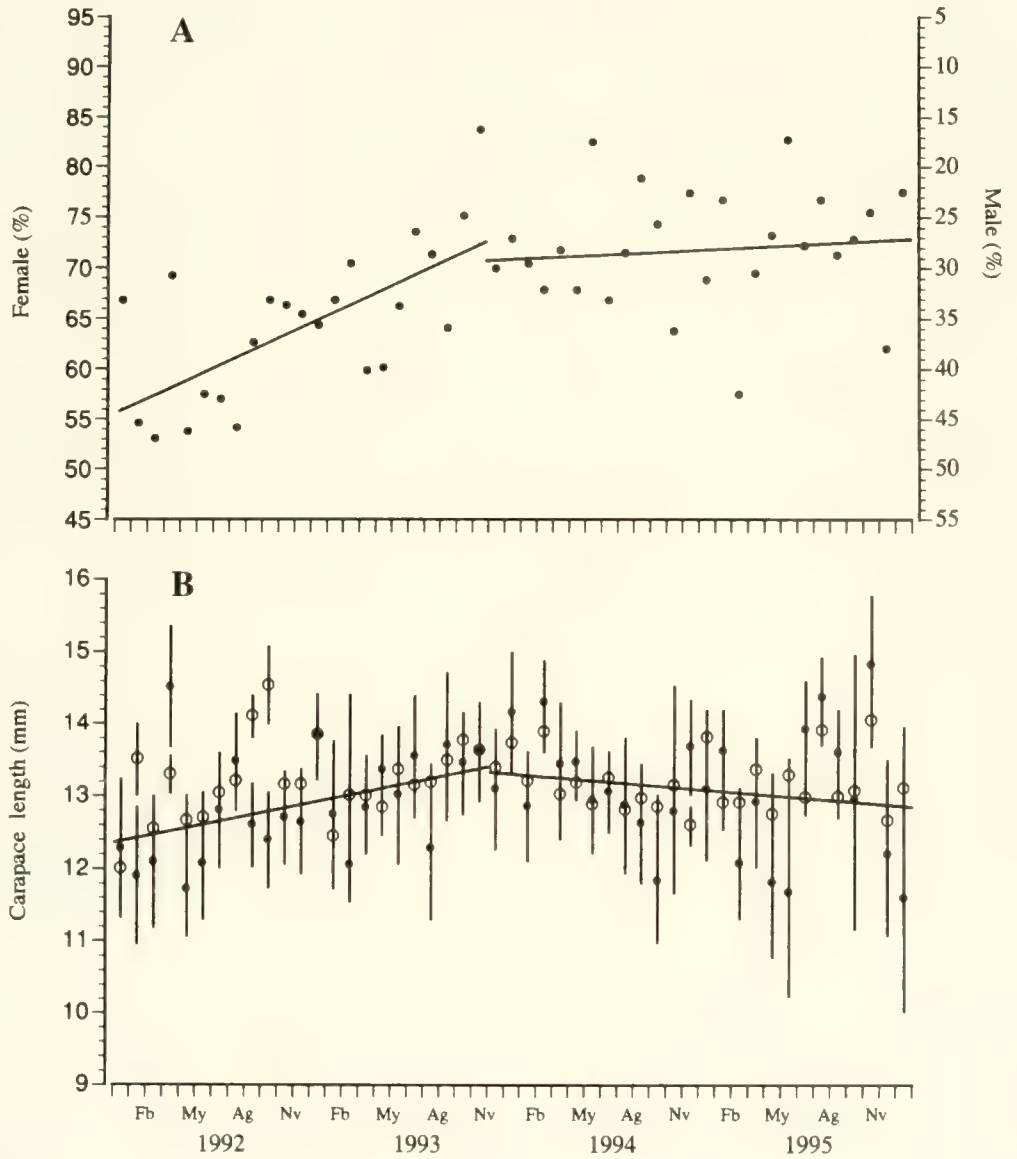

Figure 1

Sex composition (**A**) and mean carapace length (CL) (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. Mean CL is shown separately for males (closed circles) and females (open circles); vertical lines define 95% CI. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was selected to minimize the sum of squares of residuals.

Development of ovaries reached maxima in the quarter prior to peak occurrences of ovigerous females and either coincided with or immediately followed the quarter in which lowest ambient salinities occurred (Fig. 3, A, C, and D). Examined as a monthly value pooled over the three years that it was monitored (Fig. 5C), this index of ovarian development was at minimum values in June and July when ovaries of many spent and immature females, although evident for the full length of the abdomen, were limited in width to narrow translucent-yellow strands. Ovaries became deep yellow to yellow-orange as relative ovarian width began to increase markedly in August, concurrent with an annual decline in ambient salinity. By October, ovaries of most mature females were somewhat lobate in shape and yellow-orange to reddish orange in color, and ovarian index reached high values that persisted through

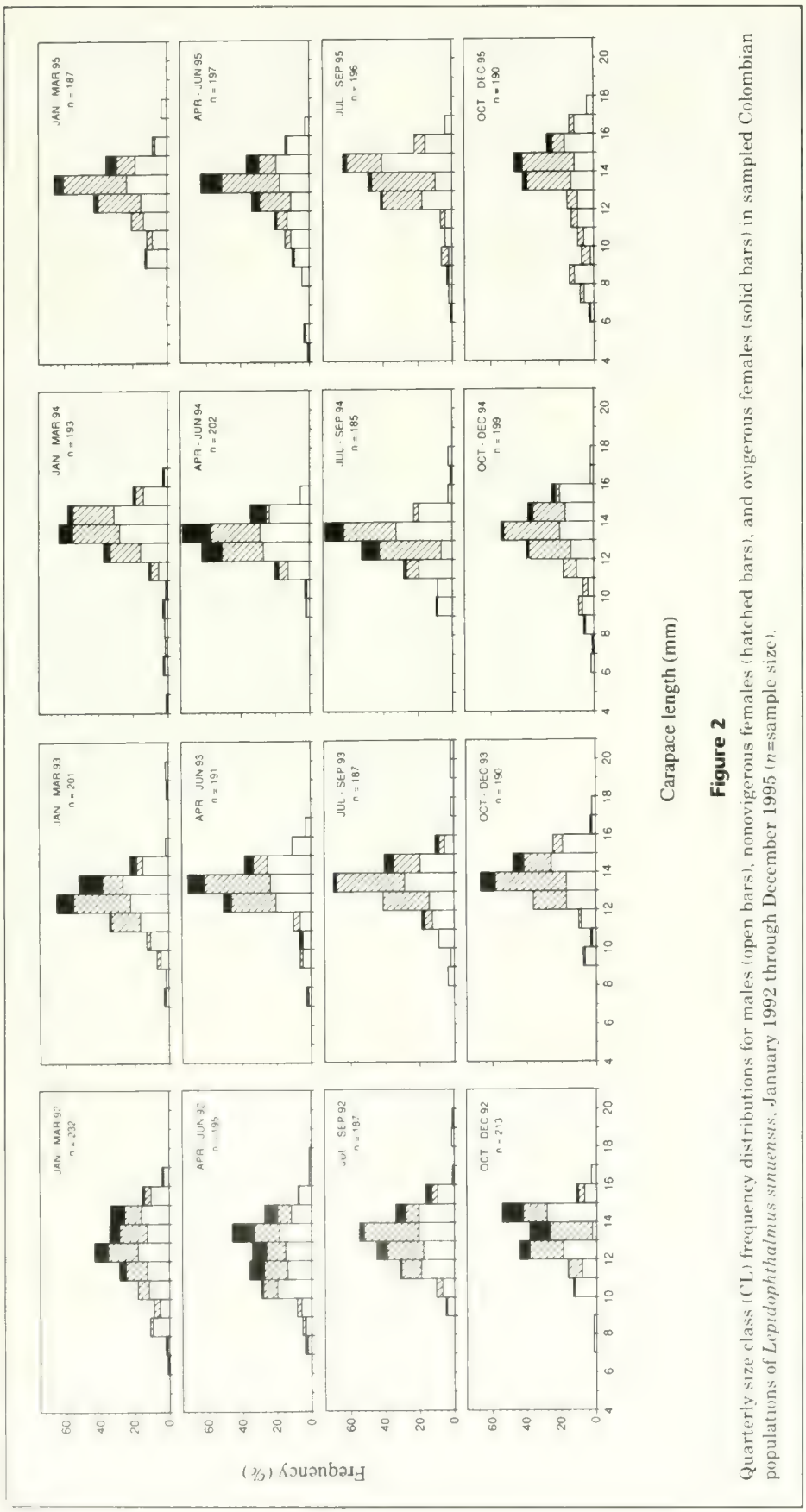

Figure 2

Quarterly size class (CL) frequency distributions for males (open bars), nonovigerous females (hatched bars), and ovigerous females (solid bars) in sampled Colombian populations of *Lepidophthalmus sinuensis*, January 1992 through December 1995 (*n*=sample size).

February. Highest values for the ovarian index, in February (0.139 ±0.012), were significantly greater than were preceding values in December or those that followed in March through May. Decreasing measures of relative ovarian width during April through June (Figs. 3C and 5C) were coincident with the second quarter maxima in abundance of ovigerous females (Fig. 3D and 5B) because many of those females had spent ovaries.

Shape of the eggs was almost spherical in recently deposited pale yellow to yellow-orange clutches and became more oblong as color faded to translucent gray-brown in late-stage eggs just prior to hatching. Mean egg volume in live late stage eggs was 0.81 ±0.07 mm^3 (n=76 eggs, from 5 different females), and the coefficient of variation in volume within a single egg clutch was 5.09% (n=30); mean dimensions were 1.22 ±0.04 mm by 1.05 ±0.02 mm. The total number of eggs per female ranged from 182 ±44 in small females (<12.0 mm CL; n=30) to 301 ±36 in large females (≤14.0 mm CL; n=141). The overall mean number of eggs for all ovigerous females collected was 251 ±18 (n=444), and the maximum number found on any single female was 958 on a specimen of 14.2 mm CL. Monthly egg counts per ovigerous female, pooled over the study (Fig. 5D), revealed peak abundances in February–April, followed by significantly lower numbers in June–July. Thus, the overall rate of egg production, when considered as a product of both abundance of ovigerous females and egg

abundance per clutch (Fig. 5, B and D), was maintained at particularly elevated levels from February through at least April and perhaps May.

Growth and sexual maturation

Size at sexual maturation in both males and females of the sampled population was evident in relative growth changes of the major chela. Asymmetry of the first pereopodal chelae was clearly evident in both sexes and did not show bias for right or left handedness in random subsamples (left:right handedness 23:27 for males, 25:25 for females; n=50 per sex). The value of this feature as a secondary sex character was suggested initially by the much heavier general appearance of the appendage in large males than in females of approximately the same size, and sexual differences in allometric growth were documented subsequently by regression analyses of morphological measurements (Fig. 6; Tables 1 and 2).

Relative growth rate in the chela width of males increased in animals that had reached a mean carapace length of at least 11.3 mm, as estimated by linear-linear piecewise polynomial regression analysis (Fig. 6A). Independent regression analysis of males larger and smaller than this size by reduced major axis revealed significant differences in slopes for those data sets (Table 1), even though the two values for this positive allometric growth did not differ significantly when compared as allometric coefficients (Table 2). When fitted by reduced major axis, regression slopes for both prematuration and postmaturation phases of growth in female chela width (Fig. 6B) differed significantly from those for both growth phases in males, although there was far greater difference between the sexes in the postmaturation phase. Relative growth in the chela width of females became significantly less positive beyond a carapace length near 10.8 mm. The negative allometric growth (coefficient <1) for this postmaturation phase in females (Table 2) differed significantly from the strongly positive allometric growth in postmaturation males.

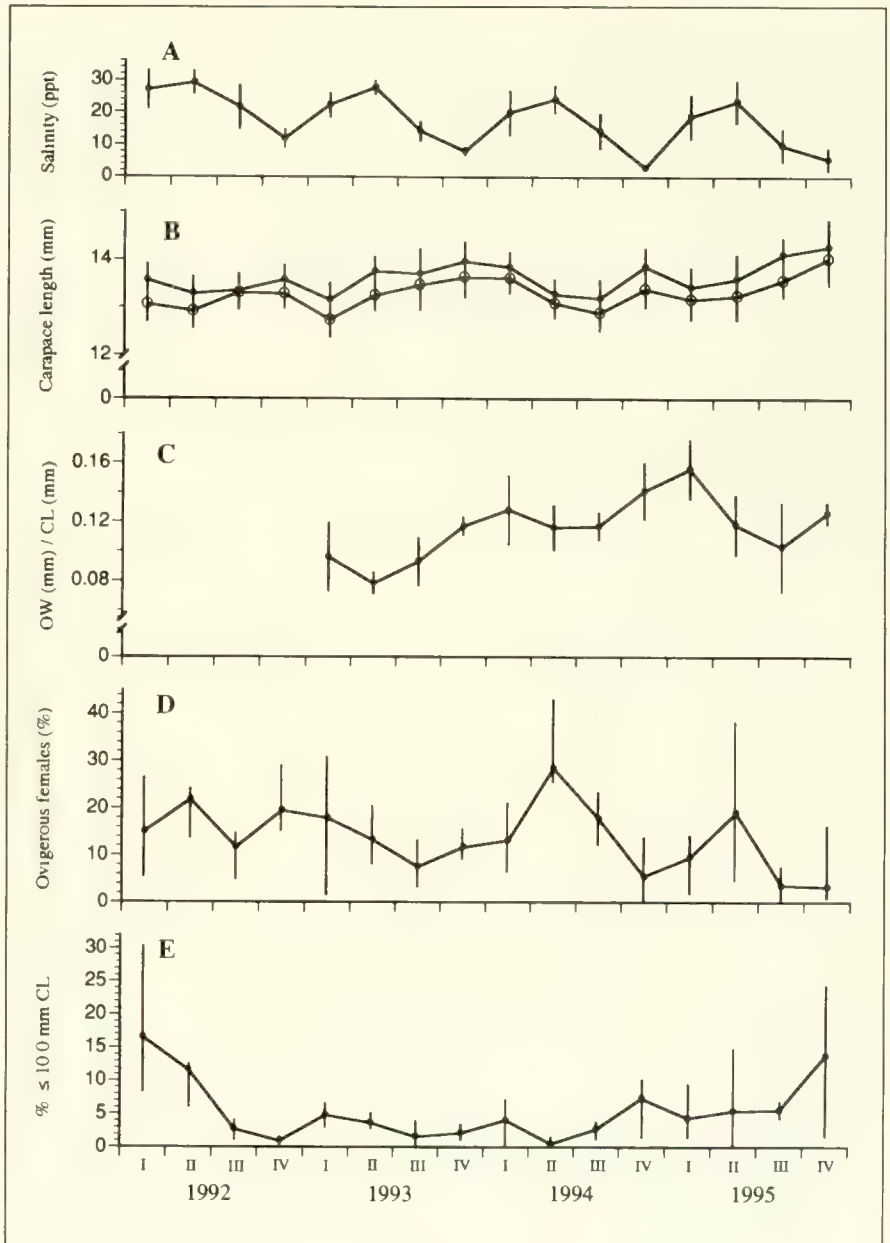

Figure 3

Quarterly measures of salinity, growth, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*, January 1992 through December 1995; for A–C, vertical lines define 95% CI; for D–E, vertical lines define range. (**A**) Morning surface salinity (ppt) at the farm intake pump station in the upper estuary, expressed as mean of daily measures throughout each quarter; (**B**) mean CL of mature (>11 mm CL) males (closed circles) and females (open circles) in sampled populations; (**C**) relative ovarian development (OW/CL); (**D**) percentage of ovigerous individuals among females; (**E**) percentage of juveniles (≤10.00 mm CL).

Analysis of relative growth in major chela height for males (Fig. 6C) and females (Fig. 6D), when scaled to carapace length, produced remarkably similar results to that for relative growth in chela width, suggesting some interdependency of those measures. Transition points were optimally located at a mean carapace length of 11.0 mm for males and 11.2 mm for females, and postmaturation growth differed significantly between the sexes (Table 1). On the basis of allometric coefficients (Table 2), positive prematuration allometric growth once again did not differ between the sexes, whereas negative postmaturation growth in females differed significantly from the strongly positive allometric growth in postmaturation males. Analysis of chela width scaled to chela height in both sexes did not indicate significant prematuration differences between males and females, and growth in both sexes was isometric or nearly so (Tables 1 and 2). However, following transition to the postmaturation phase in males, relative growth in chela width exceeded that of height. The opposite effect was seen in postmaturation females; negative allometric growth was seen in chela width, when compared to chela height.

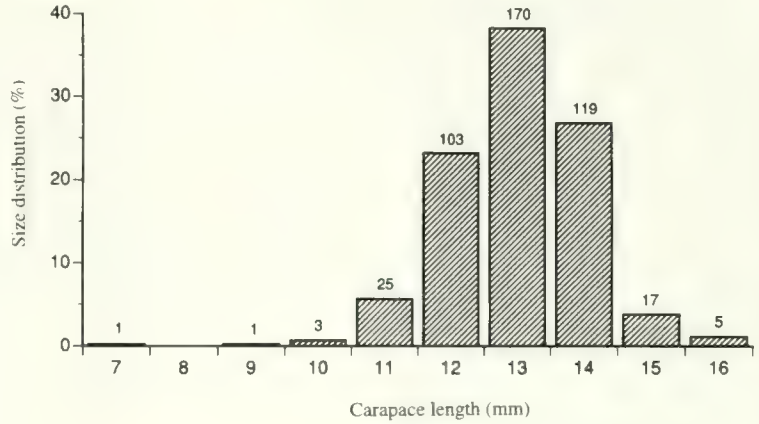

Figure 4

Size class (CL) frequency distribution of all ovigerous females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995 (number by class appears above each bar).

Analysis of total length scaled to carapace length revealed large measures of error (Tables 1 and 2), as expected in size measurements that include the length of a soft, stretchable abdomen. Allometric coefficients indicated that slopes did not significantly differentiate prematuration growth from an isometric pattern in either sex, whereas postmaturation growth on the basis of this parameter appeared to be negatively allometric but similar in rate for both males and females.

Large measures of error associated with wet weight measurements in relation to carapace length, especially at small sizes, limited detection of possible sex differences in allometric coefficients based upon this parameter and did not resolve significant differences between growth phases of either sex (Table 2). Only in the postmaturation phase were allometric coefficients based upon wet weight significantly more positive in males than in females. The more sensitive analyses of wet weight based upon regressions by reduced major axis (Fig. 7, A and B; Table 1) detected highly significant differences between postmaturation males and females, regardless of whether ovigerous females were included or excluded from the analysis, and also resolved significant differences in rates of mass accumulation between prematuration and postmaturation growth phases. Optimized transition points in piecewise regression analyses of wet weight to length relationships were near 9.8 mm CL for females and near 11.3 mm CL for males. These regression breaks suggest that maturation in males occurs at slightly higher wet weights (1.5 to 2 g) than in females (usually near 1 g).

Dry weights and ash free dry weights were determined for limited subsets of our sample and were not subjected to regression analysis. The proportional relation of dry to wet weight in ovigerous females (0.47 ± 0.06; n=8) was slightly but significantly higher than in nonovigerous females (0.36 ± 0.03; n=76) and males (0.33 ± 0.05; n=12), whereas the relation of ash free dry weight to wet weight in ovigerous females (0.052 ± 0.003; n=8) was not significantly different from that of either nonovigerous females (0.059 ± 0.011; n=41) or males (0.055 ± 0.003; n=2).

Discussion

Sex ratio

Strongly female-biased sex ratios in the monitored population of *Lepidophthalmus sinuensis* are in marked contrast to those reported in intertidal populations of *L. louisianensis* on the Mississippi coast in the northern Gulf of Mexico (Felder and Griffis, 1994), which were variable but averaged near 1:1. However, female-biased ratios have been reported in populations of *L. louisianensis* from the Louisiana coast in the northern Gulf of Mexico (Felder and

Lovett, 1989), as well as in populations of western Pacific intertidal thalassinideans such as *Trypaea australiensis* Dana (Hailstone and Stephenson, 1961), *Callianassa* s. l. *filholi* Milne Edwards (Devine, 1966), and sexually mature adult populations of *Neotrypaea californiensis* (Dana) and *Upogebia pugettensis* Dana (Dumbauld et al., 1996). Populations were male-biased in sampled populations of *Callianassa* s. l. *subterranea* Montagu from subtidal European waters (Rowden and Jones, 1994).

Observance of skewed sex ratios in thalassinidean samples may reflect actual bias in the population or an artifact of collecting methods that do not sample sexes equally within the vertical profile of burrows or across horizontal beach transections, especially when collections must be restricted to readily accessed reaches of shoreline sediments. Movement of ovigerous females toward the surface for egg release or to optimally ventilate eggs could lead to greater probability of their capture when burrows are aspirated with yabby pumps. Likewise, sampling restricted to shorelines may reflect differential positioning of sexes within the burrow along tidal or wave agitation clines. Such effects could account for previous observations in which populations of *Callichirus islagrande* were female-biased on high wave-energy beaches but not on nearby protected beaches, or for ratios that differed markedly from month to month in some populations of *L. louisianensis* from the Gulf of Mexico (Felder and Griffis, 1994). In the present study, mudflats along margins of drainage canals were fully accessible to sampling during periods of low pond discharge, samples were not limited to shorelines, and burrows were not as deep as reported for above mentioned populations of *C. islagrande* and *L. louisianensis*. From resin casts (Fig. 4 in Nates and Felder, 1998), it was observed that almost all burrows were <1 m in depth, thus encompassing water volumes readily extractable with yabby pumps.

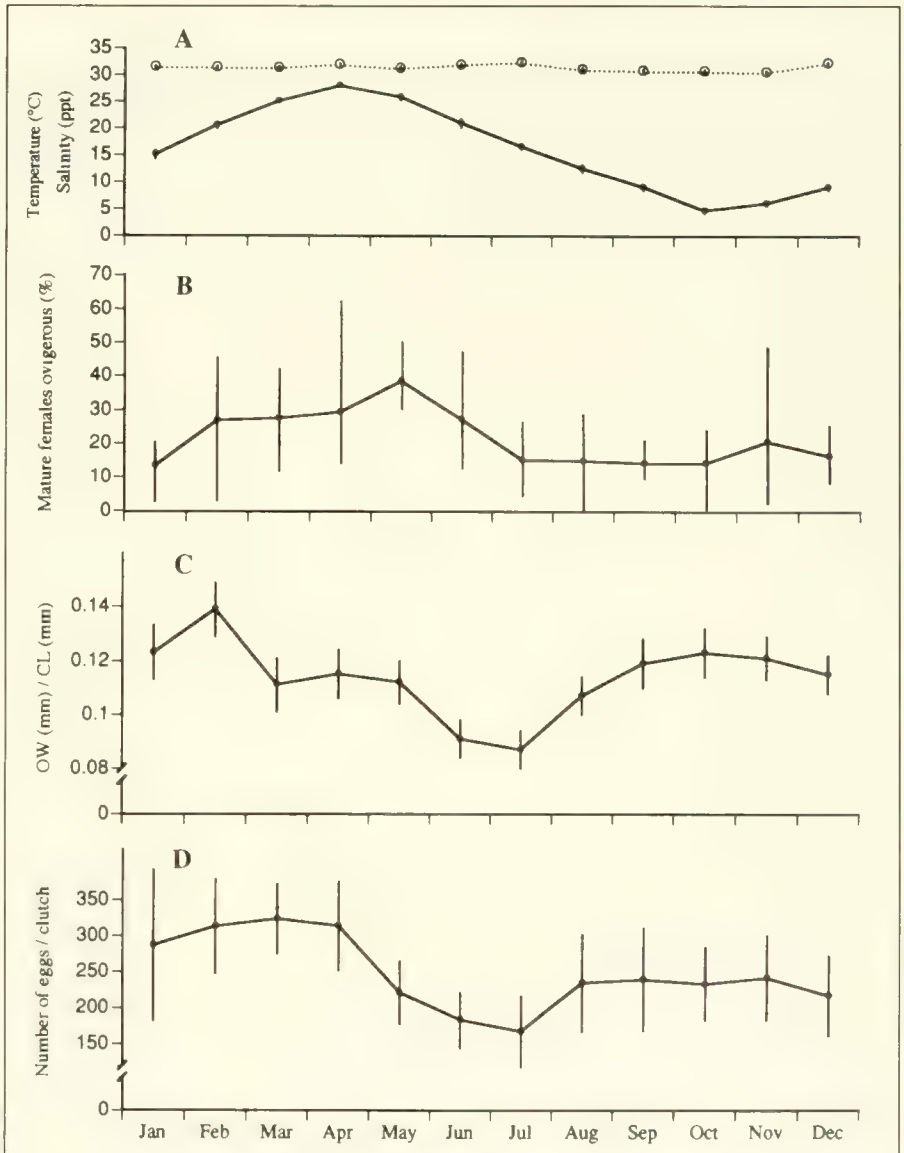

Figure 5

Pooled monthly measures for salinity, temperature, and reproductive indices in sampled Colombian populations of *Lepidophthalmus sinuensis*; for A, monthly temperature data were pooled from December 1991 through December 1993, and monthly salinity from January 1992 through December 1995; for B, monthly data were pooled from January 1992 through December 1995; for C, monthly data were pooled from January 1993 through December 1995; for A, C, and D, vertical lines define 95% CI; for B, vertical lines define range. (**A**) Morning surface salinity (solid circles, continuous line) at farm intake pump in upper estuary, and afternoon surface temperature (open circles, broken line) at outlet in pond 1, expressed as means of daily measures; (**B**) frequency of ovigerous individuals among mature (>11.0 mm CL) females of populations; (**C**) relative ovarian development (OW/CL); (**D**) mean number of eggs in clutches of ovigerous females.

Table 1

Formulae and statistics for linear regressions (by reduced major axis, with untransformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, from December 1991 through December 1995. Regressions were calculated for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), n = sample size, r^2 = coefficient of determination, 95% CI = confidence interval of slope.

	n	r^2	Formulae	95% CI
ChW:CL				
Males				
All	985	0.69	$ChW = (0.612 \times CL) - 3.474^{a}$	±0.021
$\leq X$	218	0.47	$ChW = (0.618 \times CL) - 3.179^{b}$	±0.061
$>X$	767	0.49	$ChW = (0.789 \times CL) - 5.974^{a,b}$	±0.039
Females				
All	1998	0.35	$ChW = (0.273 \times CL) - 0.519^{a,b}$	±0.009
$\leq X$	125	0.62	$ChW = (0.454 \times CL) - 1.925^{a,b}$	±0.049
$>X$	1873	0.12	$ChW = (0.304 \times CL) - 0.943^{a,b}$	±0.013
ChH:CL				
Males				
All	987	0.74	$ChH = (0.991 \times CL) - 4.843^{c}$	±0.031
$\leq X$	192	0.47	$ChH = (1.063 \times CL) - 5.012^{d}$	±0.111
$>X$	795	0.57	$ChH = (1.198 \times CL) - 7.761^{c}$	±0.054
Females				
All	1998	0.49	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.016
$\leq X$	177	0.64	$ChH = (0.842 \times CL) - 3.345^{c,d}$	±0.075
$>X$	1821	0.20	$ChH = (0.513 \times CL) - 0.425^{c,d}$	±0.021
ChW:ChH				
Males				
All	987	0.94	$ChW = (0.618 \times ChH) - 0.482^{e,f}$	±0.009
$\leq X$	274	0.85	$ChW = (0.605 \times ChH) - 0.354^{g}$	±0.028
$>X$	713	0.88	$ChW = (0.655 \times ChH) - 0.831^{e,g}$	±0.017
Females				
All	2000	0.71	$ChW = (0.532 \times ChH) - 0.292^{e,g}$	±0.013
$\leq X$	71	0.88	$ChW = (0.550 \times ChH) - 0.175^{f}$	±0.046
$>X$	1929	0.53	$ChW = (0.588 \times ChH) - 0.646^{f}$	±0.018
TL:CL				
Males				
All	1007	0.80	$TL = (4.349 \times CL) - 1.033^{h,i,l}$	±0.121
$\leq X$	737	0.77	$TL = (4.693 \times CL) - 4.695^{h,l}$	±0.161
$>X$	270	0.15	$TL = (6.374 \times CL) - 32.918^{h,j}$	±0.703
Females				
All	2158	0.64	$TL = (4.641 \times CL) - 3.186i^{j,k}$	±0.117
$\leq X$	1006	0.64	$TL = (5.419 \times CL) - 11.495^{h,i,j}$	±0.201
$>X$	1152	0.22	$TL = (5.766 \times CL) - 19.813^{k}$	±0.293
WW:CL				
Males				
All	937	0.70	$WW = (0.751 \times CL) - 6.431^{l,m,o}$	±0.026
$\leq X$	200	0.22	$WW = (0.679 \times CL) - 5.250^{n}$	±0.084
$>X$	737	0.60	$WW = (0.998 \times CL) - 9.927^{l,n,s}$	±0.046
Females (including those with eggs)				
All	1933	0.49	$WW = (0.613 \times CL) - 5.053^{l,p}$	±0.019
$\leq X$	50	0.32	$WW = (0.508 \times CL) - 3.195^{m,q}$	±0.122
$>X$	1883	0.42	$WW = (0.698 \times CL) - 6.204^{l,p,q}$	±0.024
Females (excluding those with eggs)				
All	1542	0.53	$WW = (0.581 \times CL) - 4.680^{o}$	±0.019
$\leq X$	41	0.42	$WW = (0.472 \times CL) - 2.933^{l,n,r}$	±0.119
$>X$	1501	0.44	$WW = (0.662 \times CL) - 5.767^{o,r,s}$	±0.024

[a–s] allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

Table 2

Allometric coefficients measured as slopes for linear regressions (by least squares estimate, with log-transformed data) of chela width on carapace length (ChW:CL), chela height on carapace length (ChH:CL), chela width on chela height (ChW:ChH), total length on carapace length (TL:CL), and wet weight on carapace length (WW:CL) for male and female populations of *Lepidophthalmus sinuensis* sampled at the Agrosoledad S. A. shrimp farm, upper Cispata estuary, Colombia, December 1991, through December 1995. Coefficients were determined for entire data set (All) and for data subdivided at the transition point (yielding separate regressions for data points $\leq X$ and data points $>X$, where X = size at onset of sexual maturity estimated by piecewise linear-linear polynomial regression), 95% CI = confidence interval of coefficient. ** = allometric coefficient significantly ($P<0.05$) different from 1.0. *a–u* = allometric coefficients with same superscript are significantly ($P<0.05$) different from each other.

	ChW:CL		ChH:CL		ChW:ChH		TL:CL		WW:CL	
	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI	Allom. coef.	95% CI
Males										
All	1.577**[a]	±0.059	1.457**[e]	±0.047	1.085**	±0.017	0.928**[m,q]	±0.027	3.094**[s]	±0.118
≤*X*	1.525**[b]	±0.162	1.440**[f]	±0.122	1.061**[i]	±0.039	0.968[n,r]	±0.035	2.762**	±0.747
>*X*	1.608**[c]	±0.129	1.477**[g]	±0.110	1.106**[k]	±0.033	0.618**[m,n,o]	±0.164	3.056**[t]	±0.118
Females (including those with eggs)										
All	0.820**[a,b,c,d]	±0.039	0.869**[e,f,g,h]	±0.033	0.934**[j,k,l]	±0.021	0.895**[n,o,p]	±0.025	2.476**[s,t]	±0.090
≤*X*	1.625**[d]	±0.210	1.470**[h]	±0.160	1.096[l]	±0.116	1.031[n,o,p]	±0.052	3.458**[u]	±1.102
>*X*	0.441**[a,b,c,d]	+0.053	0.491**[e,f,g,h]	±0.045	0.864**[j,k,l]	±0.033	0.693**[p,q,r]	±0.051	2.064**[s,t,u]	±0.122

This observation suggests that the detected sex bias accurately characterizes the population sampled.

In the course of previously reported observations on populations of *C.* s. l. *filholi,* it was noted that the sex ratio was near 1:1 only when small animals were included in the sample (Devine, 1966). For *L. sinuensis* there is also a correlation between mean size of animals in the monitored population and sex ratio over the four years of monitoring. As noted for *C.* s. l. *filholi*, samples of smaller mean CL were nearer 1:1 in sex ratio than were samples of larger mean CL. The trend toward increasing frequency of females reached an approximate asymptote after 23 months of observation, simultaneous with the trend in increasing CL of males, and may indicate a point at which increasing numbers of larger males established a sexual equilibrium by displacing small males from a limited habitat or maintained territory. This increase corresponds roughly to the time when burrow densities within ponds on the farm began exponential increase and when detrimental effects on water quality and penaeid production became evident (equals month 38 in Figure 1 of Nates and Felder, 1998). Sex ratios and mean carapace lengths may thus serve to forecast potential for rapid increases in infesting populations.

Both the large body size and the robust chelipeds of mature males could be of advantage in competition for limited space and available females wherever *L. sinuensis* occurs in dense, mature aggregations. Such behaviors have been suggested previously to account for large numbers of possibly displaced juvenile males of *L. louisianensis* observed periodically in plankton samples (Felder and Lovett, 1989; Felder and Rodrigues, 1993). Similar intraspecific competition for space, in which juveniles are expelled to the surface, has also been postulated to occur in some populations of *Callianassa* s. l. *japonica* (Ortmann), along with possible immigration of juveniles to other habitats (Tamaki and Ingole, 1993). While not documented to occur in *L. sinuensis*, colonization of mariculture ponds by such displaced juvenile males pumped in with estuarine waters could account for higher percentages of males observed early in our study. Such recruitment of juveniles could potentially supplement larval settlement within ponds to rapidly build early infestation densities.

Ovigerous females

The abbreviated life cycle in *L. sinuensis* includes only two brief zoeal stages, large numbers of which occur in nocturnal plankton samples taken at the study site (Nates et al., 1997). The eggs of this species and its congener *L. louisianensis* are comparable in size to those of *Callianassa* s. l. *kraussi* Stebbing, another estuarine species that exhibits markedly abbreviated development (Forbes, 1973), and are larger than those of many thalassinids with longer larval histories and wider planktonic dispersal (see

Pohl, 1946; Forbes, 1973; Tunberg, 1986), with some clear exceptions (see de Vaugelas et al., 1986). Given abbreviated development in *L. sinuensis* and the likelihood of almost immediate settlement by decapodids into the vicinity of our sample site, we expected to detect distinct cohorts of small recruits, from which we could estimate rates of growth to maturation. However, unlike the population of the warm temperate species *L. louisianensis* from the Gulf of Mexico (Felder and Lovett, 1989), tropical populations of *L. sinuensis* included ovigerous females in every month of sampling. This potential for continuous recruitment over the annual cycle, coupled with our limited success in consistently capturing small individuals, limits clear definition of reproduction and growth cycles from collections of recruits.

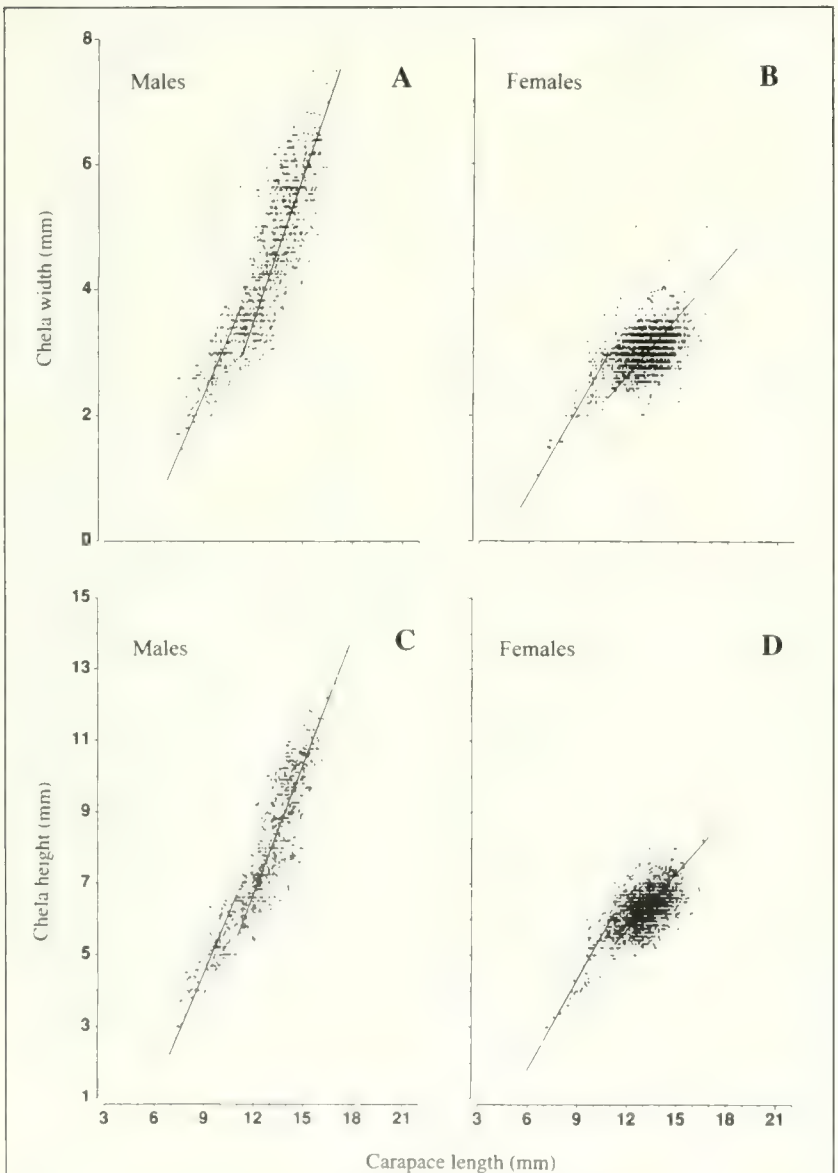

Figure 6

Linear regression (by least squares estimate for untransformed data) of chela width (ChW) on carapace length (CL) for (**A**) males and (**B**) females and chela height (ChH) on CL for (**C**) males and (**D**) females in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

Vitellogenesis in *L. sinuensis* was evident in coloration and size changes of ovaries viewed through a translucent region of the cuticle, as in other thalassinid species (Hailstone and Stephenson, 1961; Forbes, 1977; Felder and Lovett, 1989). The pattern of change in *L. sinuensis* over the course of maturation is as much as that reported for *L. louisianensis*, with ovaries becoming more massive and opaque as maturation advances (Felder and Lovett, 1989). However, when tracked as an annual index of reproductive activity, relative ovarian width in *L. sinuensis* at no point reached the highest mean values reported for *L. louisianensis* (even after correcting misplaced decimals in the *y*-axis of Fig. 1 of Felder and Lovett [1989]). We suggest that this reflects year-round reproductive activity in *L. sinuensis*, rather than investment in a more punctuated temperature-modulated event as might be expected in temperate latitudes. It may also account for a greater number of eggs on ovigerous females of *L. louisianensis* (598 ±212; n=4) than on ovigerous females of the year-round reproducing *L. sinuensis* (251 ±18; n=444) (Nates et al., 1997). Even so, significant fluctuations in mean values for relative ovarian width did occur over the three years that we monitored this value in *L. sinuensis*, with highest values preceding maximum abundance of ovigerous females by two to three months.

In tropical nearshore decapods, it is common to have extended periods of reproduction without distinct peaks defined by seasonal temperature (Sastry, 1983; Steele, 1988; Bauer, 1992; Mouton and Felder, 1995). However, whether modulated by temperature or other factors, an-

nual cycles in availability of nutrition may determine potential for vitellogenesis and success of larvae (Zimmerman and Felder, 1991; Mouton and Felder, 1995). Although temperature was not subject to marked fluctuation in the shrimp farm habitat of *L. sinuensis*, it did vary slightly with the annual changes in rainfall patterns that determined salinity of the upper estuary (Fig. 4A). The annual decline in salinity from April through October reflected increased input of nutrient-loaded waters from the nearby Río Sinú which was reported to result in periodic elevation of penaeid shrimp growth rates on the Agrosoledad farm (Mogollón[1]). Similarly, such low salinity periods may have produced improved conditions for vitellogenesis in *L. sinuensis*. Peak development of ovaries in the first quarter of the typical year either coincided with or shortly followed lowest mean salinity during the last quarter of the previous year, and fell markedly just after salinity peaked. The abundance of ovigerous females peaked almost simultaneously with salinity in most years of the study and a decrease in mean ovarian width immediately followed, indicating that the abundance of females with spent ovaries was not offset by other females simultaneously undergoing vigorous ovarian development. Reduced vitellogenesis following the high salinity period was also suggested by the markedly reduced mean number of eggs per clutch found in those ovigerous females that occurred from May through July.

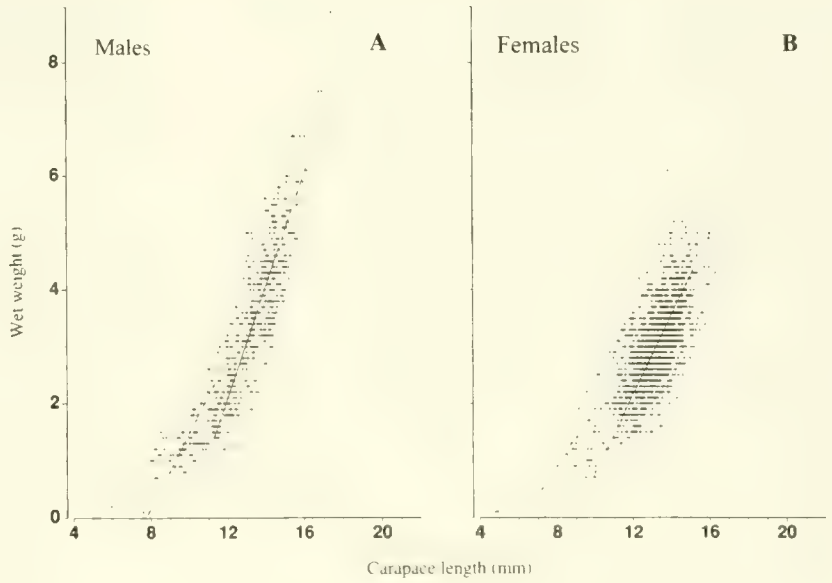

Figure 7

Linear regression (by least squares estimate for untransformed data) of wet weight (WW) on carapace length (CL) for males (**A**) and females (**B**) in sampled Colombian populations of *Lepidophthalmus sinuensis*, December 1991 through December 1995. The transition point at which data are subdivided, estimated by piecewise linear-linear polynomial regression, was positioned to minimize the sum of squares of residuals.

Growth and sexual maturation

Among callianassids and other thalassinid shrimp, the major chela is used commonly for aggressive interactions between captured individuals that are held together or among individuals encountering one another where burrows intersect in laboratory fossoria (MacGinitie, 1934; Pearse, 1945; Rodrigues, 1976; Tunberg, 1986; Felder and Lovett, 1989; Pillai, 1990; Rowden and Jones, 1994). Contrary to the case with many other genera, both males and females of *Lepidophthalmus* have one chela enlarged, but the major chela of mature males is much more strikingly developed than that of mature females (Felder and Rodrigues, 1993; Felder and Manning, 1997). Sexual dimorphism of the chelae in decapods is generally thought to reflect adaptations for their use, especially by males, in combat, display, and courtship (Hartnoll, 1974). The enlarged chela can play a role in intermale competition during the precopulatory phase of the life cycle, and marked change in its allometric growth rate is frequently related to functional sexual maturity (Grey, 1979; Aiken and Waddy, 1989; Claxton and Govind, 1994; Gu et al., 1994; Robertson and Kruger, 1994). This is likely also the case in *L. sinuensis*, even though we can only speculate as to the exact role this appendage plays in such fossorial populations.

A striking transition takes place in rate of relative growth for the major chela in *L. sinuensis*, and there is an allometric divergence between males and females in the shape of this appendage at sizes that exceed a defined, transitional carapace length. For the most part, the relationships of slopes above and below these transition or maturation points are similar to relationships previously reported in monitored

[1] Mogollón, J. V. 1995. Agrosoledad S. A., Playa de la Artillería no. 33–36, Cartagena, Columbia. Personal commun

populations of *L. louisianensis* from the northern Gulf of Mexico (Felder and Lovett, 1989). In relative growth parameters of the major chela, when scaled to carapace length, males and females of both *Lepidophthalmus* species are much more similar to one another at sizes below transition points than at sizes exceeding those points.

The estimated maturational transition size in male *L. sinuensis* ranges from 11.0 to 11.3 mm CL, whether based upon regression analysis of relative growth in chela width, chela height, or wet weight. The range of these values is markedly less than that reported in *L. louisianensis* (≥15.5 mm CL), a warm-temperate congener (Felder and Lovett, 1989). In all of these measures, postmaturation growth rate in males is more positively allometric and significantly greater than postmaturation growth rate in females, as has been shown in many other decapods (Hartnoll, 1978, 1982). Although relative weight increases were positively allometric in both males and females of mature size, the positive allometry of growth in size of the major chela, accompanied by sex-dependent changes in its shape, appears to account for postmaturation rates of weight increase in males that significantly exceeding those of females. Weight accumulation due to massive but episodic development of ovaries in maturing females would appear to be somewhat offset by the simultaneous trend toward negative allometric growth of the major chela.

Estimated from the major chela measurements, the mean maturational size in female *L. sinuensis* ranges from 10.8 to 11.2 mm CL, or slightly less than that of males but very near the values reported for females of *L. louisianensis,* which ranged from 10.7 to 11.0 mm CL (Felder and Lovett, 1989). Because over 99% of the ovigerous females we collected were ≥11.0 mm CL, the general validity of this mean size estimate for maturation appears to be confirmed on an independent basis, even though two atypically small ovigerous females <10.0 mm CL, were collected (Fig. 4). Our regression analysis of wet weight indicated that the transitional maturation point for females fell near 9.8 mm CL, but error appeared to be high in values surrounding this point. A relatively large range and error in this weight-dependent value should perhaps be expected because two variables, negative allometry of the major chela and growth of the ovaries, are likely influencing it in opposite ways. We suggest that the aforementioned annual salinity variations and the simultaneous effects on nutrient loading may seasonally alter rates of ovarian growth. This could in turn contribute to the range of weight dependent values for maturation or account for occasional occurrences of small egg-bearing females by favoring early maturation of young cohorts.

Management summary

Those penaeid culture ponds on the Caribbean coast of Colombia that operate at higher salinities than those near the Río Sinú have not been found to harbor detrimental infestations of *Lepidophthalmus*. However, nutrient-rich, estuarine waters are believed to yield high rates of penaeid production, promoting location of several major penaeid farms in oligohaline habitats that harbor natural populations of *L. sinuensis*. This pest is introduced to culture ponds by pumping in larvae and perhaps migrant juveniles from the estuary. Although filtration of influent water should serve to limit entry of any migrant juveniles, it is practical to limit entry of much smaller planktonic larvae only by carefully avoiding pumping in of waters from the estuary during nocturnal hours of peak larval activity in the water column (Nates et al., 1997). Because we herein document that *L. sinuensis* reproduces year-round, this diel restriction of pumping schedules cannot be limited solely to the first annual quarter of elevated salinity when peak abundances of ovigerous females suggest that high densities of larvae might be present among nocturnal plankton. However, such periods would almost certainly present the greatest risk of larval introductions to culture ponds.

Although controlling water influx may limit colonization of ponds from surrounding environments, *Lepidophthalmus* will almost certainly over time succeed in becoming established in estuarine ponds that provide it with both richly organic muddy substrates and annual cycles of water quality that favor reproduction. Detrimental effects become obvious when densities in ponds exceed 200 burrow openings/m^2 or 66 animals/m^2 (Nates and Felder, 1998), levels we have never found in natural settings on in the Río Sinú estuary. Explosive reproduction within the ponds appears to immediately precede problem levels of infestation, and measurements of the sex ratios and CL of the population may serve to forecast the potential for such an event. Because attainment of a strongly female-biased sex ratio is roughly coincident with previously reported exponential population growth (Nates and Felder, 1998), both sex ratio and density of mature females may prove useful predictors of population growth potential. Maturity of both males and females can be determined by measures of CL and cheliped dimensions, or by inference from burrow diameters, and immediately pending episodes of egg deposition can be predicted by monitoring the ovarian index.

Dense infestations of *Lepidophthalmus* in Colombian shrimp culture ponds have to date been treated periodically by farm operators with the carbaryl pes-

ticide Sevin®, a practice unlikely to change in the absence of proven alternative management strategies. From our observations, such applications have usually been contained within drained or slightly filled culture ponds and limited only to control of excessive thalassinid densities. It is possible that reductions in frequencies of such applications can be achieved by timing of treatments to pre-empt reproductive peaks or by limiting pesticide applications only to infestations that are found to include high percentages of mature or near-mature females, such as we observed in this study most often in the fourth annual quarter. Any measure that reduces application rates and frequencies may lessen ecological risks and contribute to effectiveness of carbaryl degradation prior to flushing treated ponds into surrounding environments.

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Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean

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Abstract.—The frequency with which dolphins from the northeastern offshore stock of the pantropical spotted dolphin, *Stenella attenuata*, experience chase and capture by tuna purse-seiners in the eastern topical Pacific Ocean was estimated by comparing dolphin school-size frequencies in sighting data from research vessel observer records, with those recorded in set data by tuna vessel observers. The objective of the study was to provide a preliminary basis for estimating stock-wide effects of fishery-induced disturbance in these dolphins.

Our analyses indicate two major characteristics for this stock: first, capture frequency appears to increase rapidly with increasing school size, and second, approximately half of the stock at any given time occurs in schools smaller than those apparently preferred by purse-seiners. This implies that if individual dolphins have a preference for associating with schools of a particular size, then individuals associating primarily with large schools would be subjected to chase and capture much more frequently than those associating with small schools. However, because the largest schools are relatively rare and account for a small percentage of individuals, the majority of dolphins in the stock would experience relatively few captures per year, although some would experience a high rate. It is not known whether dolphins do indeed exhibit such a preference, or if instead individuals associate with schools from a wide range of sizes at different times.

Schools of 1000 or more dolphins are estimated to be set on approximately once a week each on average, but such schools are estimated to represent just under one tenth of the animals in the northeastern offshore stock. Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, are estimated to be set on between two and eight times each per year and are estimated to include approximately one third of the stock. An estimated one half of the stock occurs in schools smaller than 250 animals; schools of this size are estimated to be set on less than twice per year each.

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Tuna fishermen in the eastern tropical Pacific Ocean (ETP) commonly catch large yellowfin tuna (*Thunnus albacares*) by locating a school of dolphins visually and then surrounding it with a large purse-seine net in order to capture the tuna that are often closely associated with ETP dolphin schools. The dolphins are released from the net and the tuna are then loaded aboard (NRC, 1992). This method, known as "fishing on dolphin," historically has been a significant cause of dolphin mortality (NRC, 1992) but has also recently been suggested as a significant cause of fishery-related physiological stress in the dolphins involved, perhaps to the point of causing unobserved mortality or changes in reproductive success (e.g. Myrick and Perkins, 1995).

Although it has not been possible to measure physiological stress directly in these dolphins, it is possible to use existing data to estimate how often an animal experiences chase and capture. Capture frequency provides at least a rough measure of the amount of fishery-induced disturbance that dolphins affected by the ETP tuna fishery experience. Here, we estimate capture frequency for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*) (Dizon et al., 1992). This is the species most commonly associated with tuna and historically most often used in fishing on dolphin (greater than 70% of dolphin sets annually for about the last 30 years (e.g. IATTC[1]).

A simple calculation (see "Discussion" section) leads to a rough estimate for the mean number of times an individual dolphin is set on per year of (number of dolphins set on) ÷ (number of dolphins) ≈ 8 times per year. However, simply knowing the overall average rate of capture is not sufficient to evaluate the potential adverse effects on individuals because the rate for different animals may vary widely, depending on a number of interrelated factors including school size, geographic location, time of year, and the amount of tuna associated with a school. In this paper, we investigate the effects of school size. Specifically, we show that large dolphin schools (more than several hundred animals) are much more likely to be captured than are small schools (less than one hundred animals) because of a tendency for fishermen to concentrate their effort on larger schools, which tend to carry more tuna, and to virtually ignore smaller ones. However, this result does not directly give the capture rate for an

[1] IATTC. 1992. Annual report: 1990. Inter-American Tropical Tuna Commission, La Jolla, CA, 261 p.

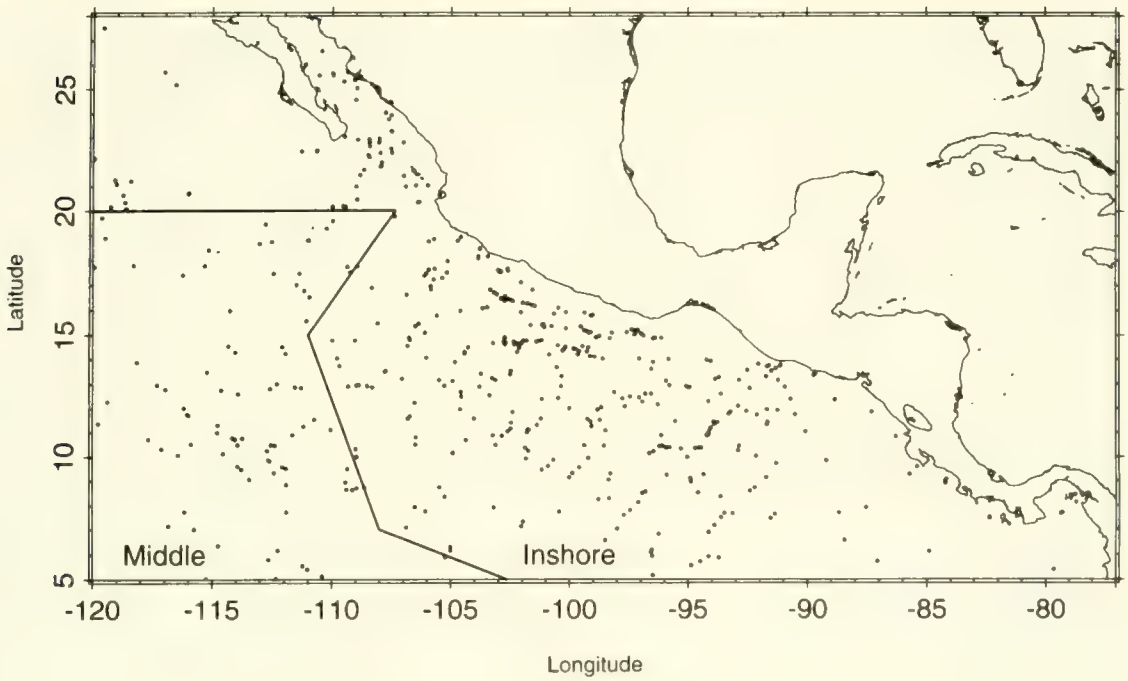

Figure 1

Geographic stock boundaries for the northeastern offshore stock of the pantropical spotted dolphin (*Stenella attenuata*). The stock is defined by the region in the ETP north and east of 5°N and 120°W, bounded at 28°N. The two strata pictured are based on those defined by Holt et al. (1987). The inshore and middle strata have total areas of 4,544,000 km^2 and 2,019,000 km^2, respectively. Points represent on-effort sightings from the research vessels, 1986–90 and 1992–93.

individual dolphin because animals may associate with schools of different sizes at different times. We consider implications for individual dolphins in the "Discussion" section.

Data and methods

To quantify the tendency for purse-seiners to set on large schools, we compared the relative frequency with which different sizes of schools are selected by fishermen for encirclement with the relative frequency with which schools of various sizes occur naturally. First, we estimated the probability distribution of sizes for spotted dolphin schools within the geographic boundaries of the northeast (NE) offshore stock[2] (Fig. 1), using observations from research vessels. This distribution models the relative number of schools of each size in the study area. Then we fitted a smooth probability distribution to dolphin school sizes from tuna vessel sets. This distribution models the relative number of times schools of each size were set on. Finally, we used the ratio of the two estimated density functions, suitably scaled, to estimate the average number of times per year a dolphin school of a given size was set on. This estimated effect includes not only the tendency of fishermen to preferentially set on larger schools, but also any tendency to search in areas where large schools may be more prevalent.

Research vessel sighting data

In 1986, the U.S. National Marine Fisheries Service (NMFS) initiated a multiyear research program to monitor trends in the abundance of dolphin populations in the ETP. The program used research vessels to conduct line transect surveys in the ETP and record sightings of all cetaceans encountered (Wade and Gerrodette, 1993). The surveys were designed to provide a spatially unbiased sample of the survey area and to be as similar as possible across years. Typically, three independent observers estimated school size and species composition for each sighting. For detailed descriptions of the survey design, materials, and methods, see Holt et al. (1987), Hill et al. (1991), and Mangels and Gerrodette (1994).

The research vessel data used in this study consisted of spotted dolphin school sightings from the

[2] Coastal and NE Offshore stocks of the pantropical spotted dolphin exist sympatrically: however, schools are for the most part distinguishable.

Table 1

Summary of research vessel data by year and stratum. Search effort is defined as the distance travelled along the trackline as observers actively search during a sea state of Beaufort 5 or less. Sighting rate is defined as the number of northeastern offshore spotted dolphin schools sighted on-effort, within 5.5 km of the ship's trackline, per 1000 km of search effort. Middle and inshore strata are defined in Figure 1.

	Inshore stratum		Middle stratum		Pooled	
Year	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate	Search effort (km)	Sighting rate
1986	9260	6.26	3457	4.92	12,716	5.90
1987	8523	7.27	4322	5.09	12,845	6.54
1988	6303	6.98	3371	3.26	9674	5.69
1989	8375	9.67	3996	4.00	12,371	7.84
1990	7036	8.10	4744	3.79	11,780	6.37
1992	10,189	5.99	0	—	10,189	5.99
1993	7953	6.29	584	3.42	8537	6.09

1986–90 and 1992–93 marine mammal surveys (Table 1). These seven surveys each occurred between 28 July and 10 December, referred to here as the "study period." We used sightings only from search effort within the NE offshore stock boundaries, for which observers were actively searching ("on-effort") and for which Beaufort sea state was 5 or below. We excluded sightings farther than 5.5 km from the trackline because school size estimates were generally unreliable for such distant schools. A total of 499 sightings were included in this study.

The median estimated school size was 106 dolphins; 48% of the estimates were less than 100, and only 1% greater than or equal to 1000 (Fig. 2A). These quantities are not corrected for size selection bias (see "Statistical model" section). The true distribution of school sizes was estimated to include a larger percentage of small schools.

Tuna vessel set data

Since the late 1970s, the Inter-American Tropical Tuna Commission (IATTC) and NMFS have placed trained observers aboard a significant percentage of ETP tuna purse-seiner vessels larger than 400 tons capacity. A single observer is placed aboard a vessel when a trip is selected for observation. These observers collect data on the dolphins with which commercial species of tuna in the ETP commonly associate, and monitor dolphin mortality due to purse-seine fishing operations. For a more detailed description of the observation programs, see IATTC (1989), IATTC,[1] or Jackson (1993).

Detailed observer data were available from tuna sets made by U.S. vessels. From these data, we used observer estimates of school size and species composition from spotted dolphin schools set on by tuna vessels within the NE offshore stock boundaries and during the study period for the years 1986–90. We used the observer's final "best" estimates, made after the set, which included counts of any animals that evaded or were cut out of net encirclement[3] (IATTC, 1991; NMFS, 1992). The tuna vessel data used here included only schools that were actually set on, and not observations of schools that were sighted but not set on. We assumed that there was no "observer effect" on a captain's choice of schools to be set on. A total of 3454 set observations were included in this study (Table 2).

The tuna vessel set data represent about 77% of the search effort during the study period for the U.S. purse-seine fleet (29 to 40 vessels during the years 1986–90). To increase search efficiency, tuna vessels often travel at 15 knots, and crews use helicopters and communicate in "code groups" (Orbach, 1977) in addition to searching with binoculars from the ship. Not all schools that are sighted are set upon, and thus the observed sets represent a much larger effective sample size in terms of sightings, and the "missing" schools tend to be small. The median estimated size of schools that were set upon was 560 dolphins. Only 4% of the estimates were less than 100, whereas 26% were greater than or equal to 1,000 (Fig. 2B).

[3] Using the pre-encirclement school size means that although we are estimating the rate at which schools of a given size were set on, it is likely that some dolphins involved in a given set were chased by the tuna vessel and its speedboats but not actually encircled by the purse-seine net. For the purposes of estimating numbers of sets as a measure of adverse impact, we do not distinguish chase from capture.

Data from individual sets made by non-U.S. vessels were not available; however, count data summarizing observed numbers of sets and trips made by all vessels were available. From these data, we used the numbers of sets on the target stock observed each year, by both U.S. and non-U.S. vessels, during the study period and for the entire year (Table 2). Additionally, the total annual number of fishing trips that involved sets on dolphins has been estimated each year from tuna vessel logbook data (e.g. IATTC[1]). Dividing the annual number of observed trips by the annual total number of trips gives the annual trip sampling fraction ("coverage"), which we took as known exactly. We further assumed that observer coverage was constant throughout the year and took the sampling fractions as applicable for the study period as well as the entire year.

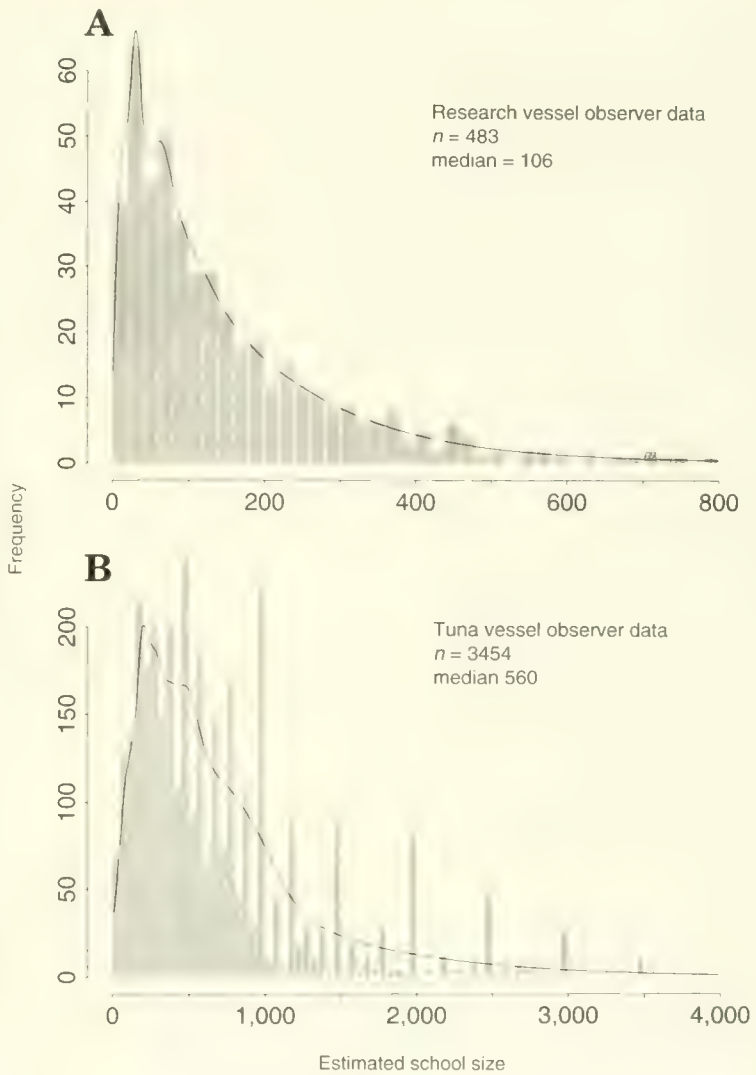

Figure 2

Estimated observed school sizes for northeastern offshore spotted dolphins. These data include observations from both geographic strata. The fitted lines are kernel density estimates (see text) for these observations. Note the different x- and y-axis scalings. (**A**) Research vessel sightings, 1986–90 and 1992–93. These data are the mean observer estimates and are not corrected for size selection bias (see text). They include on-effort sightings with perpendicular distance <5.5 km; 8 observations >800 are not shown. (**B**) Tuna vessel sets, 1986–90; 19 observations >4000 not shown.

Statistical model

We modeled the true population of NE offshore spotted dolphin schools within the stock boundaries as an independent identically distributed (i.i.d.) sample of unknown size from a hypothetical infinite superpopulation of schools having a smooth probability density for their school sizes. To characterize the true population of school sizes, both the total number of schools, $N_{schools}$, and the probability density from which their school sizes were drawn, $\pi(s)$, needed to be estimated. Although school size is really a discrete quantity, we approximated it using a continuous-valued random variate.

Dolphin school sightings are made from visual clues such as surface disturbances or associated bird flocks, and larger schools in general provide a more visible target. Thus, the sighting probability for schools at a given range depends on school size, leading to a selection bias (relative to $\pi(s)$) towards larger schools in the research vessel observations. We modeled these observations as a biased sample of size $n_{schools}$ from the true population. Because the ships' tracklines were random with respect to the dolphin population, we assumed that there were no other selection biases. We denoted the probability density of observed school sizes by $\pi^*(s)$ to distinguish it from $\pi(s)$, and note that

$$\pi(s) = \frac{w_{eff}}{w_{eff}(s)}\pi^*(s),$$

where $w_{eff}(s)$ = the line transect effective strip halfwidth for schools of size s ; and

w_{eff} = the size-averaged effective strip halfwidth (Appendix D in Burnham et al., 1980).

Table 2

Summary of tuna vessel data by fleet, year, and stratum. Coverage is defined as the percentage of fishing trips, involving sets on dolphins by vessels over 400 tons, that carried a scientific observer. Coverages and annual numbers of trips are taken from IATTC Annual Reports (e.g. IATTC, see Footnote 1 in main text). Observed sets per trip is defined as the mean number of observed sets on northeastern offshore spotted dolphin schools for trips that involved sets on dolphins. Middle and inshore strata are defined in Figure 1.

			Observed sets per trip 28 Jul–10 Dec ("study period")				Observed sets per trip annual			
Fleet	Year	Coverage	Trips	Inshore	Middle	Pooled	Trips	Inshore	Middle	Pooled
U.S.	1986	41.7	25	9.60	1.96	11.6	43	14.4	4.53	18.9
	1987	91.5	61	17.3	5.25	22.6	119	21.9	6.89	28.8
	1988	57.6	33	13.7	4.88	18.6	76	13.0	4.86	17.9
	1989	99.1	50	14.9	3.66	18.6	115	15.3	3.77	19.1
	1990	100.0	14	16.3	3.21	19.5	73	12.3	3.62	15.9
	Total	76.9	183	14.9	4.14	19.0	426	16.2	4.88	21.1
Intl.	1986	25.3	29	12.3	2.90	15.2	68	14.9	2.84	17.7
	1987	28.3	44	15.8	0.409	16.2	82	17.9	0.988	18.9
	1988	35.8	54	8.70	3.52	12.2	111	10.3	3.87	14.2
	1989	37.0	57	13.6	2.61	16.2	141	13.3	2.41	15.7
	1990	42.0	66	8.35	6.92	15.3	147	12.3	4.77	17.1
	Total	34.3	250	11.4	3.60	15.0	549	13.3	3.18	16.5

Both $w_{eff}(s)$ and w_{eff} depend upon the data truncation distance (Burnham et al., 1980), denoted by w and equal to 5.5 km in this analysis. $\pi^*(s)$ was estimated from the observed school sizes. However, to estimate $\pi(s)$, we also needed to estimate $w_{eff}(s)$, as described in "Estimation" section.

Anecdotal reports consistently imply that tuna vessel captains do not search for or set on dolphin schools at random when fishing on dolphin in the ETP. Because larger dolphin schools are observed to carry more tuna, they are presumably sought out and set upon preferentially, and the set data would have a selection bias towards large schools. We modeled the schools associated with purse-seine sets (both observed and unobserved) as a biased sample, with replacement, of unknown size from the true population of schools. To characterize these schools, both the total number of sets, N_{sets}, and the effective probability density from which their sizes were drawn, $p(s)$, needed to be estimated. $p(s)$ represents the superposition of the tuna fishermen's school-size selection preference upon $\pi(s)$. Sizes were recorded for all sets on trips carrying observers, and therefore there was no additional observer selection bias (in relation to $p(s)$). Assuming a random selection of trips, we treated the observed sets as an unbiased subsample of size n_{sets} and estimated $p(s)$ directly from the observed sizes. There was some concern with serial correlation between sets (see "Independence of observations" section).

Because the number of dolphin schools is not constant over time, we interpreted $N_{schools}$ as the time-averaged expected number of schools, and in particular did not use a finite population estimator. Similarly, we interpreted N_{sets} as the expected number of sets rather than making finite population estimates of the actual realized number of sets.[4]

Estimation

U.S. vessels—study period The observed school-size distributions from both the research vessel sighting data and from the tuna vessel set data were roughly lognormal in shape (Fig. 2). We estimated $\pi^*(s)$ and $p(s)$ using an adaptive kernel density estimator on the logs of the observed school sizes and then transformed the estimated density back to the original scale (Silverman, 1986). This variable bandwidth algorithm was chosen in order to make reasonable density estimates in the right tails where there were few data, while not oversmoothing near the modes. We chose the bandwidth scaling parameters as a trade-off between smoothness and fit to the data. We treated the observer estimates (mean estimates in the case of research vessel data) as exact measure-

[4] Technical details and a discussion of our estimators for $N_{schools}$ and N_{sets} can be found in Perkins, P. C., and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p.

ments and did not attempt to correct for the possibility of size estimation biases in either data set (see "Discussion" section) or use a deconvolution kernel to account for estimation variance.

Our estimates of $w_{eff}(s)$ were based on modelling the inherent selection bias in the research vessel sighting data. We used a bivariate hazard-rate detection function in a size-dependent line transect analysis of the perpendicular sighting distances and sizes of the observed schools (Drummer and McDonald, 1987; Palka, 1993). Perpendicular distances were binned to reduce the effect of rounding in the data. School sizes were not binned because we did not use a parametric model for their distribution.

We define the average capture frequency for a school of size s as

$$N_{capture}(s) = \frac{N_{sets}(s)}{N_{schools}(s)} = \frac{N_{sets}p(s)}{N_{schools}\pi(s)}.$$

Setting the observed counts $n_{schools}$ and n_{sets} equal to their expectation gives

$$n_{schools} \approx E[n_{schools}] = \left(\frac{2Lw_{eff}}{A}\right)N_{schools} \text{ and}$$

$$n_{sets} \approx E[n_{sets}] = f_{trips}N_{sets},$$

where L = the total distance searched by the research vessels;
A = the total area within the stock boundaries; and
f_{trips} = the fraction of tuna vessel trips that carried an observer.

Using the relationship between $\pi(s)$ and $\pi^*(s)$, and these moment equations for $n_{schools}$ and n_{sets}, we estimated the capture frequency for a school of size s as

$$\hat{N}_{capture}(s) = \frac{n_{sets}}{f_{trips}} \frac{2L\hat{w}_{eff}}{An_{schools}} \frac{\hat{p}(s)}{\hat{\pi}^*(s)}.$$

Note that the factor w_{eff} cancels out and only $w_{eff}(s)$ remains.

Because there were so few schools smaller than 100 animals set on by tuna vessels, and so few schools larger than 1000 animals sighted from research vessels, we restricted our analysis to schools from 100 to 1000 animals, and computed estimates of capture frequency at intervals of 100 animals.

Stratification and pooling There were many school size data from tuna vessel sets (n_{sets}=3454), however, there were far fewer research vessel sighting data ($n_{schools}$ = 499) and these had an uneven spatial distribution. We decided that research vessel sightings were too sparse to stratify our estimates of $\pi^*(s)$ and $w_{eff}(s)$ geographically. We did make stratified estimates of $p(s)$, but this had very little effect in absolute terms on the estimates of capture frequency, and so we present only pooled estimates for simplicity.

Similarly, we did not stratify by year in any of our estimates. Set data, trip sampling fractions, sighting data, and search effort were combined to make a single estimate of the average N_{sets} and $N_{schools}$ over all years.

Extrapolation to the international fleet and to annual estimates Data from individual sets came only from U.S. tuna vessels, so that estimating capture frequency due to the entire fleet required extrapolation. We made the assumption that a captain's preference for dolphin school sizes upon which to make sets did not vary with the vessel's country of origin and thus extrapolated our estimate of $p(s)$ to the entire fleet. Our estimates of total numbers of target sets were based on separate observed counts and sampling fractions for the U.S. and the international fleets,

$$\hat{N}_{sets} = \hat{N}_{sets}^{(US)} + \hat{N}_{sets}^{(Intl)} = \frac{n_{sets}^{(US)}}{f_{trips}^{(US)}} + \frac{n_{sets}^{(Intl)}}{f_{trips}^{(Intl)}}.$$

This expression was substituted in for (n_{sets}/f_{trips}) in our estimates of capture frequency for the combined fleet. For non-U.S. vessels, we had only the total number of target sets observed, and we were unable to estimate the variance in $\hat{N}_{sets}^{(Intl)}$. Thus, our estimates for the combined fleet do not include estimates of precision.

Our estimates of capture frequency are strictly valid only for the study period. However, if we assume that the same patterns in school sizes and captain's preference for school sizes hold for the entire year, then the annual capture frequency can be estimated by using the corresponding annual set counts for U.S. and non-U.S. vessels. Because we had only the total number of target sets observed during times other than the study period, our estimates of annual capture frequency do not include estimates of standard error.

Independence of observations

Because of the geographically correlated nature of consecutive research vessel sightings or tuna vessel sets, successive school size observations from a single vessel may not have been independent. This is particularly a concern for the set data, because of the possibility of repeated sets on the same school (see

"Discussion" section). Although dependence does not add a bias to our estimates, it does decrease the effective sample size, which affects our estimates of precision. We accounted for this problem by using bootstrap standard error estimates, and by defining our bootstrap resampling units so as to make them as independent as possible while keeping a reasonably large sample size. For research vessel data, we took days as the resampling unit; for tuna vessels, we resampled by trips. For each bootstrap iteration, we resampled from the research vessel data to achieve approximately the same amount of search effort in each stratum as was actually achieved. We resampled from the tuna vessel data to achieve exactly the actual observed number of trips.

Results

Estimated distribution of school sizes

Figure 2 shows the kernel estimates of the densities $\pi^*(s)$ and $p(s)$. Both estimated densities were much smoother at large school sizes than at small school sizes. This is partially due to the variable bandwidth in the kernel estimator, but primarily due to the data themselves.

Estimated effective strip halfwidth

Figure 3 shows the estimated values for the effective strip halfwidth as a function of school size. Because $\pi^*(s) \propto w_{eff}(s)\pi(s)$, $w_{eff}(s)$ represents the relative amount of "thinning" for schools of different sizes, i.e. $w_{eff}(s)/w$ is the probability of a school of size s being detected from the research vessel, given that it is within the truncation distance w. The estimated values indicate that approximately one third of schools of size 100 within the truncation distance (5.5 km) were missed by the research vessel observers, and essentially all schools of size 1000 were detected. The result shown in Figure 3 is, qualitatively at least, partially constrained by the bivariate line transect model, i.e. if the data indicate dependence of detectability upon school size, then the parametric form for $w_{eff}(s)$ dictates that the estimated curve must vary smoothly and monotonically with size and must approach w asymptotically. However, the model fit need not have any dependence on school size, and the specific direction and rate of increase shown in Figure 3 are due to the data, and agree with observer experience in terms of reaching the limiting value within the range of sizes shown.

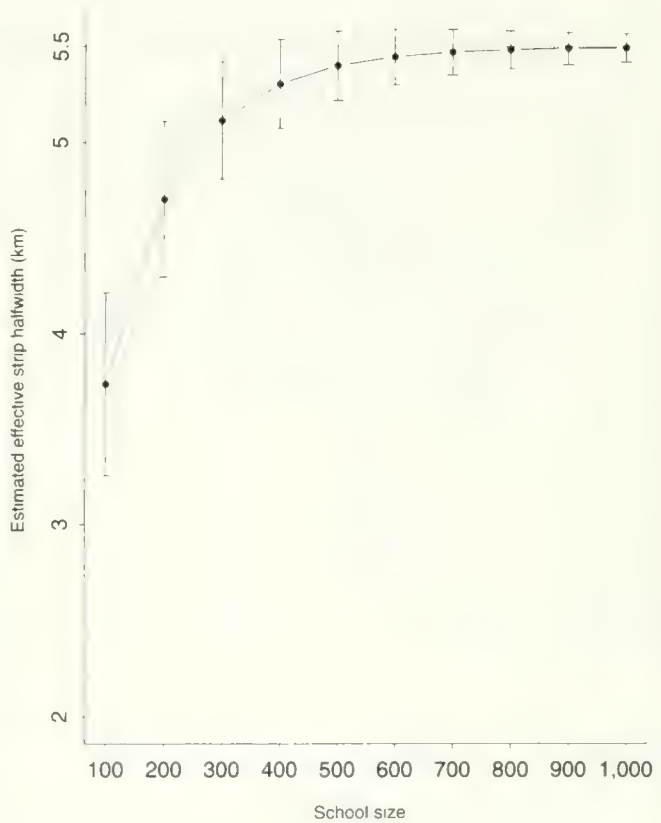

Figure 3

Estimated effective strip halfwidth as a function of dolphin school size. These maximum likelihood estimates are from the bivariate hazard rate line transect model as discussed in the text, and are based on northeastern offshore spotted dolphin school sightings from observers aboard NMFS research vessels during the months July to December, 1986–90 and 1992–92. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals. The horizontal line at 5.5 km indicates the perpendicular truncation distance in the line transect model.

The standard error bars in Figure 3 exceed w in some cases, although it is not possible for $w_{eff}(s)$ to exceed the truncation distance w. These error bars are presented simply to represent the estimated precision for each estimate, and should not be interpreted as confidence intervals. Confidence intervals for the estimated halfwidths would tend to be asymmetric and would not exceed the truncation distance.

Estimated capture frequency

Figure 4 shows the estimated capture frequency due to U.S. tuna vessels. These estimates represent the average number of times a school of a given size was set on each year during the study period. The esti-

mates are an integration of the information presented in Figure 2 and Figure 3, i.e.

$$\hat{N}_{capture}(s) \propto \hat{w}_{eff}(s)\hat{p}(s)/\hat{\pi}^{*}(s),$$

scaled by a suitable estimate of the overall average capture frequency. The magnitude and direction of the trend in $\hat{N}_{capture}$ was almost entirely due to the estimates of $p(s)$ and $\pi^{*}(s)$. Estimates of the factor $w_{eff}(s)$ varied only by about 50% over the range of sizes considered, whereas the estimated ratio of $p(s)$ to $\pi^{*}(s)$ varied by two orders of magnitude.

The precisions of our estimates of capture frequency depended on the precisions of the individual estimated factors involved in $\hat{N}_{capture}(s)$. We were able to estimate those different precisions using the output of the bootstrap procedure and found that they varied widely. Much of the variability was in our estimates of $\pi^{*}(s)$, with bootstrap estimates of CV ranging from 9% at a school size of 100 up to 24% at 1000. Bootstrap CVs for $\hat{w}_{eff}(s)$ were low, ranging from 13% down to 1%, but, as mentioned above, $w_{eff}(s)$ was the factor most constrained by the model. Bootstrap CV's for $\hat{p}(s)$ were lower than those for $\hat{\pi}^{*}(s)$, ranging from 14% at a school size 100 down to 6% at 1000. Set counts and sighting counts both had bootstrap CV's of approximately 6.5%.

Figure 5 shows the estimated annual capture frequencies due to the U.S. fleet and due to the combined U.S. and international fleet. The estimate of the combined capture frequency for schools of size 1000 is 36.1 sets per year, or one set every 10 days, compared with well under once a year for schools of 100 animals. The estimate for the median school size set on (560 animals) was 10.1 sets per year, or just under once per month. The U.S. fleet accounted for an estimated 31% of sets during the years 1986–90. Although we were not able to estimate standard errors in these annual estimates, the error bars in Figure 4 should give at least a rough idea of the potential precision.

Because of the extrapolation of school-size distributions necessary to make annual and combined fleet estimates, the two curves in Figure 5 are identical in shape to that in Figure 4, but have different scale factors. The scale factor for the lower curve was an estimate of the overall (size-averaged) annual capture frequency, $N_{sets}/N_{schools}$, due to the U.S. fleet, whereas the scale factor for the upper curve was the corresponding estimate for the combined fleets. These two overall capture frequency estimates were not extrapolated from data collected during the study period, but were based on annual set counts for the two fleets.

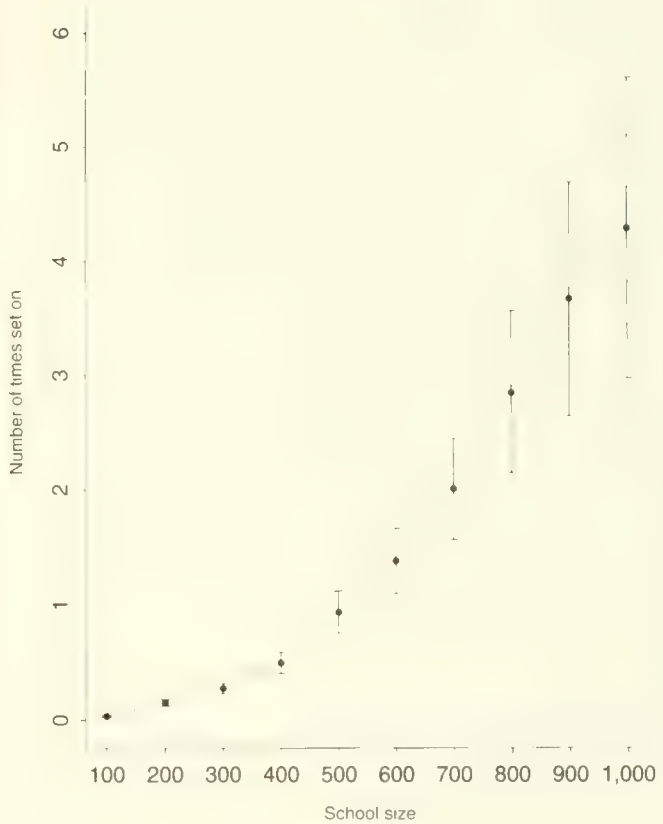

Figure 4

Estimated capture frequency as a function of dolphin school size, for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by U.S. tuna purse-seiners, between 28 July and 10 December (19.4 weeks), for the years 1986–90. Error bars indicate plus or minus one standard error and should not be interpreted as confidence intervals.

Using the estimated school sizes from the sighting data, and weighting by the estimated effective strip width, $w_{eff}(s)$, we estimated the cumulative percentage of individual dolphins in schools greater than or equal to a given size, i.e.

$$H(s) \equiv \Pr\{\text{a dolphin is in a school of size} \geq s\}$$

$$= \int_{s}^{\infty} t\pi(t)dt \Big/ \int_{0}^{\infty} t\pi(t)dt$$

$$\hat{H}(s) = \frac{\sum s_i \hat{w}_{eff}(s_i) I\{s_i \geq s\}}{\sum s_i \hat{w}_{eff}(s_i)},$$

where $I\{s_i \geq s\} = \begin{cases} 1, & \text{if } s_i \geq s \\ 0, & \text{otherwise} \end{cases}$

and the sums are over research vessel sightings.

Combining $\hat{H}(s)$ with the combined-fleet capture frequency estimates (Fig. 5, upper curve), schools of 1000 animals or greater were estimated to be set on at least once every ten days and contained an estimated 9% of dolphins (Fig. 6). Schools set on most often by tuna purse-seiners, containing from about 250 to 500 dolphins, were estimated to be set on between 2 and 8 times each per year on average; these schools represented just under an estimated one third of the stock. An estimated one half of NE offshore spotted dolphins occurred in schools smaller than 250 animals; schools of this size were estimated to be set on less than twice per year each.

We note that $H(s)$ should not be used to quantify the school size preferences of individual dolphins. For example, although we estimated that schools larger than 1000 animals contained an estimated 9% of dolphins at any given time, this does not imply that the same 9% of dolphins always made up such schools.

Capture frequency for very large schools

Although no kernel estimate of $\pi(s)$ was possible for s greater than 1000 animals, the estimated detection probability for those schools was essentially one out to the truncation distance w, making a rough calculation for capture frequency possible. Because of the rounding tendency of tuna vessel observers, we made an estimate for schools greater than or equal to 1000. With the assumption that the effective strip halfwidth is equal to the truncation distance, an estimate of the average capture frequency due to the entire fleet is

$$\hat{N}_{capture}(s \geq 1000) = \frac{\hat{N}_{sets}^{large}}{\hat{N}_{schools}^{large}}$$

$$= \frac{n_{sets}^{(US,large)}}{n_{sets}^{US}} \left(\frac{n_{sets}^{US}}{f_{trip}^{US}} + \frac{n_{sets}^{Intl}}{f_{trips}^{Intl}} \right) \frac{2Lw}{An_{schools}^{large}} .$$

The estimated average capture frequency for these very large schools was 51.3 sets per year, or just under once a week.

Discussion

Capture rates for individual dolphins

To interpret these capture frequency results in terms of individual dolphins, we must consider the size range of the schools with which a given individual tends to associate. If one assumes that dolphins have a strong fidelity for a characteristic school size, then the above results indicate that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets, whereas the majority of dolphins were subject to relatively little disturbance from the fishery. However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and a range of other assumptions are possible.

If school membership is completely fluid and dolphins mix perfectly among schools, then over the long term, all dolphins would experience the same capture rate. We made a rough estimate of this rate by estimating the total annual number of dolphins set on and the total number of dolphins. Using data from Table 2, we made a rough estimate of 7610 for the

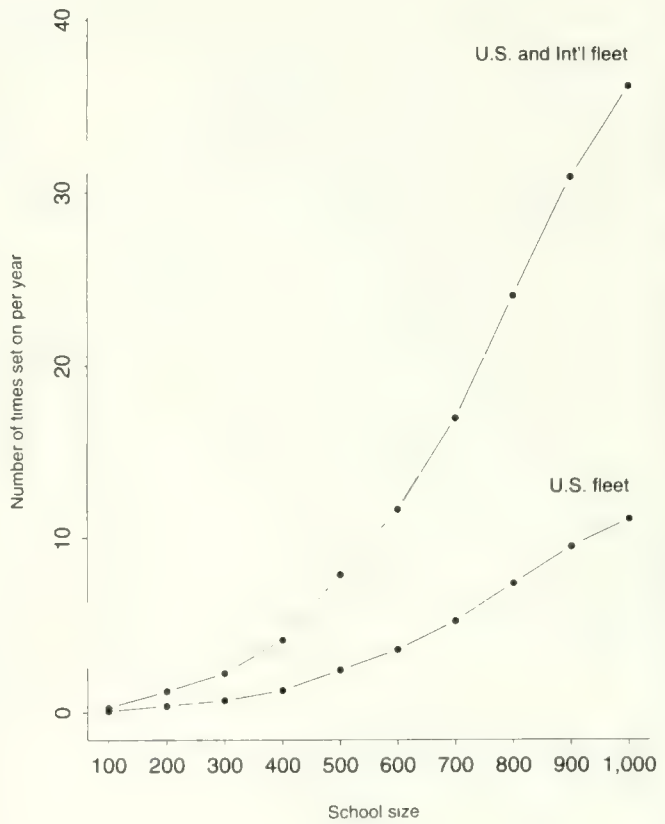

Figure 5

Estimated annual capture frequency as a function of dolphin school size for schools of northeastern offshore spotted dolphins. The estimates are of the average number of times a school was set on each year by tuna vessels in the ETP purse-seine fleet for the years 1986–90. The lower curve shows the number of sets due to U.S. vessels only; the upper curve shows the number of sets due to U.S. and non-U.S. vessels combined. Estimates of standard error were not possible for these estimates.

mean annual number of sets on NE offshore spotted dolphins during the period of this study. From tuna vessel observer data, an estimate for the mean school size for those sets is 773 animals. When combined with an estimate for the total number of NE offshore spotted dolphins (Wade and Gerrodette, 1993), this gives (7610 × 773 dolphins set on) ÷ (731,000 dolphins) = 8.04 sets per dolphin per year.

The true picture certainly lies between these two extremes. On the other hand, if the composition and spatial location of some large schools are static over periods of weeks or longer, then animals in those schools could be subject to short-term capture rates even higher than those of our estimates because of the clustered distribution of fishing effort.

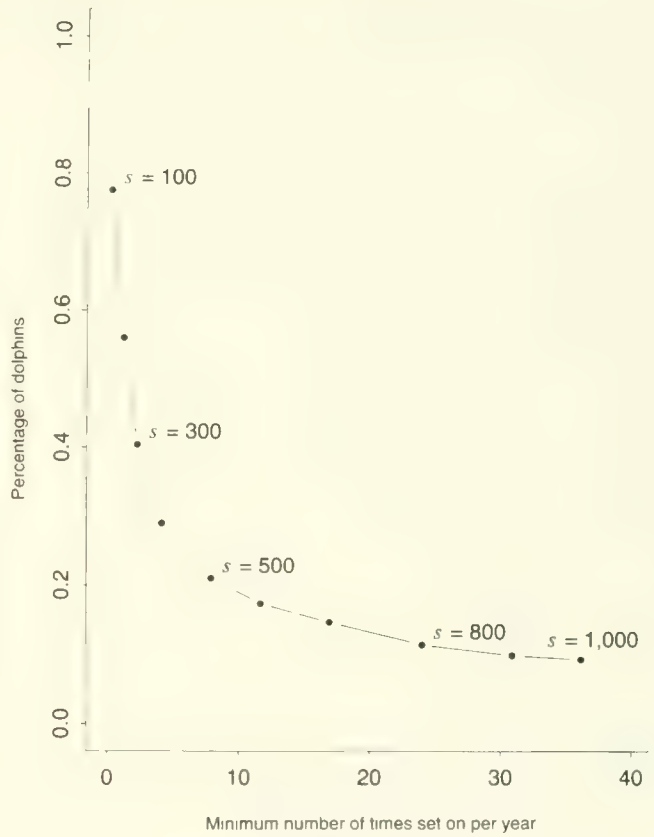

Figure 6

Estimated percentage of northeastern offshore spotted dolphins subject to different levels of capture frequency. The horizontal axis represents the minimum number of times a dolphin school is set upon per year by U.S. and non-U.S. tuna vessels in the ETP purse-seine fleet, for the years 1986-90. The vertical axis represents the estimated fraction of the stock (not the fraction of schools) subject to at least that rate of being set upon. s is the minimum school size accounting for that percentage.

Geographic stratification

Holt et al. (1987) partitioned the ETP into several geographic strata primarily on the basis of spotted dolphin density as observed from tuna vessels during years prior to the study period. In an alternate analysis for capture frequency, we used Holt et al.'s partition to fit separate densities for $p(s)$ in each of two strata (Fig. 1), and used separate counts n_{sets} and $n_{schools}$. The estimates of $p(s)$ from the two strata were significantly different (Kolmogorov-Smirnov goodness-of-fit test, P=0.002), but primarily at smaller school sizes, less than 200 animals, and this stratification made little difference in absolute terms from the unstratified estimates of capture frequency. The similarity in capture frequency estimates between strata indicates that fishing pressure was approximately proportional to dolphin school density.

We did not stratify geographically to estimate $\pi^*(s)$ or $w_{eff}(s)$ because we found that the number of observations in the middle stratum ($n_{schools}$=81) was too small to allow stratification and still have reasonable precision. A Kolmogorov-Smirnov test and Q-Q plots indicated that there was no substantial difference (P=0.62) in $\pi^*(s)$ between strata for the research vessel observers. On the other hand, we fitted the bivariate line transect model to data from the two strata separately and found that the estimate of $w_{eff}(s)$ for the middle stratum was 10–20% smaller than that for the inshore stratum, depending on school size. However, there were few data on which to base either result. One reason why $w_{eff}(s)$ might actually have differed between the two strata was a difference in observed sea state conditions; a higher average Beaufort sea state was reported in the middle stratum. The practical impact is that our estimates of capture frequency may have been overinfluenced by data from the inshore stratum.

Observer size-estimation errors

Our statistical model for the school size data included terms for selection biases, that is, which schools were included in the sighting or set data. However, there was also a potential for observer size-estimation biases. That is, given a sighting of, or a set on, a specific school, an observer had to estimate size of the school. The results presented here treated the observer estimates as exact counts. We did not include an error term for size estimates in either the kernel density estimates of $\pi^*(s)$ and $p(s)$ or the bivariate line transect estimates of $w_{eff}(s)$.

An observer size estimation bias would scale or otherwise deform those estimates of $\pi^*(s)$ or $p(s)$ (or both), depending on whether the bias was proportional to size or was more complex. Even if the observers were unbiased in their individual estimates, estimation variance would still increase both tails in the density estimates. Thus, if research vessel observers and tuna vessel observers consistently made different errors in estimating school sizes, then the trend in our estimates of capture frequency, e.g. Figure 4, could have been in part or entirely due to those errors.

Gerrodette and Perrin[5] studied dolphin school size-estimation errors for research vessel observers by ground-truthing observer estimates against aerial photo counts of the same school. They found that the counts from a single observer could be modeled as lognormally distributed given the true school size. They also found that a given observer in the study might have a substantial positive or negative bias.

Using their photo and observer dataset, we fitted a lognormal model for the geometric means of the observer estimates from each sighting.[6] The fit indicated that the observers had essentially no bias at a true school size near 100, but that there was a negative bias of 21% at a school size of 1000. Because the lognormal is a skewed distribution, this mean bias corresponds to essentially no median bias. The estimated CV for the estimates, given the true size, was 48%.

Given this information, it would have been possible in theory to correct the research vessel observer estimates for bias. However, we did not make that correction because the corresponding correction for the tuna vessel set data was not possible in the absence of a suitable ground-truth study. Significant differences between observers and observing conditions on research vessels and tuna vessels precluded the assumption that any size-estimation biases are similar in the two types of data.

Spatial distribution of schools and school sizes

Our analysis can be taken to imply full spatial mixing, that is, all schools of a given size within the stock boundaries (or within each stratum for the stratified case) have the same probability of being set upon. A more realistic model is that some schools have a higher or lower probability depending not only on their size but also on their geographic location in relation to areas of high school density or high fishing effort. Other factors, such as seasonal effects and the amount of associated tuna, are also interrelated with location in determining the rate of capture for a given school. Because we included only limited spatial information in our model, the appropriate interpretation of our results is that we estimated an average probability of being set upon, as a function of school size, for schools within the stock boundaries (or each stratum).

Observer experience suggests that pressure from fishing on dolphin can reduce average dolphin school size, i.e. areas of high fishing effort tend to have smaller schools.[7] This decrease in school size may be a result of chase and capture operations during sets intentionally or unintentionally splitting schools into smaller subgroups.[8] However, we did not find any indication of such a trend in our NE offshore spotted dolphin school-size data. We concluded that if fishing pressure did affect spotted dolphin school size, its effects may have been masked by size selection in the tuna vessel set data and by the relatively limited number of observations in the research vessel sighting data.

Dolphin schools

Variation in school size over time The simplest interpretation of this analysis would assume that a dolphin school is a fixed entity that does not change in size. If, on the other hand, a school is not a well-defined entity over any length of time, i.e. schools often fragment and reaggregate (e.g., Scott and Cattanach, 1998), then defining capture frequency for anything other than an individual dolphin becomes problematic. The superpopulation model that we used is one way to account for this fluid nature of dolphin schools. In particular, the research and tuna vessel school-size data represent time-averaged samples, i.e., averages over repeated realizations from the superpopulation. Estimated capture frequencies can be interpreted in terms of short-term rates.

Species composition Most schools in both the research vessel and tuna vessel data included not only NE offshore spotted dolphins, but other species as well, primarily spinner dolphins (*Stenella longirostris*). We did not differentiate between pure and

[5] Gerrodette, T. and C. Perrin. 1991. SWFSC Admin. Rep. LJ-91-36, Southwest Fisheries Science Center, La Jolla CA, 74 p.

[6] Details of this exploratory analysis can be found in Perkins, P. C. and E. F. Edwards, 1997, SWFSC Admin. Rep. LJ-97-03, Southwest Fisheries Science Center, La Jolla CA, 36 p

[7] Rasmussen, R. 1997. Southwest Fisheries Science Center, La Jolla, CA. Personal commun.

[8] Hall, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Some limited data have been collected to study school fragmentation and reaggregation (Perrin et al., 1979; Scott, M. 1997. Inter-American Tropical Tuna Commission, La Jolla, CA. Personal commun.

mixed schools in our analysis. Thus, we took as our population of schools not just those composed purely of NE offshore spotted dolphins, but all schools containing them. School sizes were taken as the total number of animals in each school. This approach would not have been appropriate if we had been estimating a stock-specific abundance (e.g. Wade and Gerrodette, 1993). However, as long as there is no bias in the species composition of schools that are set on, our approach is valid. An exploratory data analysis indicated that the distribution of species proportions was very similar for both research and tuna vessel data.

There was some indication that pure spotted schools tended to be smaller on average than mixed spotted-spinner schools. We did not pursue this because it did not affect our results.

Encounter rate for very large schools

Inspection of Figure 2 raises the question of why so few very large schools (1000 animals or greater) were sighted from the research vessels when so many were set upon by tuna vessels. Only five schools (1% of sightings) in that range were reported by research vessel observers, and the largest was estimated to be 2617 animals. In that range, 896 schools (26% of observed sets) were reported set upon by tuna vessel observers, and 97 were estimated to be larger than 2617 animals. These largest schools from the set data did tend to include slightly higher percentages of species other than spotted dolphins. However, they were still primarily made up of spotted dolphins (just over an estimated 70% on average), and it was not the case that they were due to an association with large groups of, for example, common dolphins (*Delphinus delphis*), which are known to form very large schools (e.g. Edwards and Perrin, 1993).

At least four explanations for this apparent discrepancy are possible. First, this may simply reflect the tuna vessel captains' preference for setting on large schools. Second, the difference may be due to relative bias in size estimation between the two types of observers, as discussed earlier. However, to explain all of the difference, the two sets of observers would have to differ on average by a factor of five in their estimates. Third, the research vessels may have missed a relatively rare segment of the population of schools, which the tuna vessels are able to seek out with a much greater search effort and a nonrandom search strategy. Fourth, some of these large observations in the set data may have been from intentionally repeated sets on the same schools. There is evidence in the tuna vessel observer data for both of these last two explanations, i.e., that localized areas of high density or school size (or both) may exist and that repeated sets on a single school may occur.

Conclusions

The results of this study indicate that tuna purse-seiners in the ETP fishing on NE offshore spotted dolphins have a strong preference for setting on larger than average dolphin schools, and that such schools were subject to being set on at a much higher rate than were smaller schools. Specifically, the largest schools considered, those of 1000 or more animals, were estimated to be set on approximately once every week, whereas the smallest schools considered, those of 100 animals, were estimated set on less than once a year. Our estimated capture rates should be taken as averages for a given school size and do not account for variation due to other factors, such as geographic location or the amount of associated tuna. Also, although we estimated rates in terms of sets per year, we do not assert that the short-term capture rate for a given school is constant, i.e. that sets occur at evenly spaced intervals throughout the year. For example, relatively few sets are made "on dolphin" in the NE offshore stock range during June and July (e.g. Edwards and Perkins, 1998).

These results do not account for any errors in estimation of dolphin school size. Although potential errors in school-size estimates made by research vessel observers were investigated, no corresponding study of potential errors for tuna vessel observer estimates was possible.

To draw conclusions about capture frequency for an individual dolphin, we must consider the size range of the schools with which a given individual tends to associate. Our results imply that dolphins associating primarily with large schools will be subjected to capture much more often than individuals associating primarily with small schools. However, we also estimated that the largest schools are relatively rare and account for a minority of the total number of individual dolphins at any given time. These results may imply that a fixed but relatively small percentage of the dolphin population was consistently subjected to a high rate of capture in purse-seine nets but that a majority of dolphins occur in schools smaller than those apparently preferred by purse-seiners, and experience relatively few captures per year.

However, little is known about the spatial and temporal dynamics of dolphin schools and their sizes, and other conclusions are possible. If dolphins associate with a wide range of school sizes, then the capture rates for individual dolphins would tend to "av-

erage out" and thus would vary less than the range of capture rates for schools. On the other hand, differences between schools in factors other than size could lead to short-term individual capture rates that are even higher than our estimates.

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Regional and temporal variability in growth and mortality of bay anchovy, *Anchoa mitchilli*, larvae in Chesapeake Bay

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Abstract.—Temporal and spatial variability in growth and mortality rates of bay anchovy, *Anchoa mitchilli*, larvae was analyzed in Chesapeake Bay. Larvae were collected in cruises during June and July 1993, on transects spaced at 18.5-km (10 nmi) intervals over the entire bay. Growth and mortality rates were estimated in lower, mid, and upper bay regions and analyzed in relation to environmental variables, predators (biovolumes of the scyphomedusa *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*), and larval prey (zooplankton abundances). Otolith increment analysis indicated that the mean baywide growth rate of larvae increased significantly from 0.59 mm/d in June to 0.72 mm/d in July. The baywide mortality rate of larvae declined from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July. In each month, regional mortality rates were highest in the lower bay. Regionally, mortality ranged from a low of 0.14 (13.1%/d) in the upper bay in July to a high of 0.54 (41.7%/d) in the lower bay in June. Mortality rates declined with increasing larval size. Stage-specific survival was both size-specific and growth-rate dependent as indicated by trends in mortality (M), weight-specific growth (G), and the M/G ratio. Growth rates were positively correlated with temperature and zooplankton abundance. Larval abundances, but not mortality rates, were negatively correlated with gelatinous predator biovolumes. Recruitment potential of bay anchovy was judged to be highest in July in the lower third of Chesapeake Bay. Although lower, production of anchovy prerecruits in June and in other Bay regions was substantial and contributed significantly to prerecruit abundances in 1993.

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In highly fecund fishes that spawn serially over a protracted season and a broad geographic range, variable patterns of cohort successes and failures may result that not only lead to fluctuating recruitments but that are difficult to detect in the absence of sampling programs that are temporally and spatially intensive. We estimated temporal and regional variability in larval-stage growth and mortality of bay anchovy (*Anchoa mitchilli*), an abundant (Hildebrand and Schroeder, 1928) and highly productive species (Newberger and Houde, 1995; Wang and Houde, 1995) in Chesapeake Bay. In exploratory analyses and simulations, Houde (1996, 1997b) demonstrated that variability in recruitment success of bay anchovy can occur when stage-specific mortality rates vary during early life. Recently, individual-based models of bay anchovy dynamics in Chesapeake Bay have demonstrated how stage-specific mortality and growth processes may operate and how density-dependent regulation could dampen fluctuations in abundance (Wang et al., 1997).

Bay anchovy are an important component of the Chesapeake Bay food web. They are not commercially exploited but are a major prey of harvested species such as bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and striped bass (*Morone saxatilis*) (Hartman and Brandt, 1995) and may represent up to 90% of piscivorous fish diets seasonally (Baird and Ulanowicz, 1989). Spawning by bay anchovy is widespread in the Bay and occurs over a broad range of temperatures and salinities (Dovel, 1971; Houde and Zastrow, 1991). Bay anchovy is a pelagic, serial spawner (Luo and Musick, 1991; Zastrow et al., 1991) that spawns most intensively from May through August in Chesapeake Bay, where it may account for 96–99% of fish egg and 67–88% of larval catches (Olney, 1983). During peak spawning, densities of eggs frequently range from 10 to >1000/m^3 and densities of larvae from 1 to >100/m^3 (Olney, 1983; Dalton, 1987; Dorsey et al., 1996; MacGregor and Houde, 1996; Rilling and Houde, manuscript in review). Within a spawning season, regions of highest egg and larval abundances may shift, as they did from the upper to the lower bay between June and July 1993 (Rilling and Houde, manuscript in review). Such shifts may have important repercussions for bay anchovy production and for production of other fish species and inverte-

brate predators that rely upon bay anchovy as prey.

Because bay anchovy eggs and larvae, and its gelatinous predators, peak in abundance during summer, temporally and spatially variable predation is potentially a significant factor controlling bay anchovy survival and recruitment. Results of mesocosm experiments (Cowan and Houde, 1993) have indicated that up to 20–40% of bay anchovy eggs and larvae in Chesapeake Bay during the peak spawning season may be consumed daily by jellyfish. Purcell et al. (1994) analyzed jellyfish gut contents and estimated that these predators could account for up to 21% of the daily egg mortality and 41% of the larval mortality of bay anchovy in Chesapeake Bay. In site-specific studies, Dorsey et al. (1996) estimated that jellyfish accounted for 0–35%/d of egg mortality, and from 0 to 15%/d of yolksac larval mortality.

Minor variability in daily mortality or growth rates in a 30–50 d period during early life, can generate tenfold or greater differences in recruitment potential of marine fish (Cushing, 1975; Houde, 1987, 1989b). Previous studies in Chesapeake Bay have documented variability in anchovy egg and larval abundances and yolksac larval dynamics at regional scales (Dorsey et al., 1996; MacGregor and Houde, 1996), but this study is the first to provide a comprehensive overview of larval dynamics for the entire Chesapeake Bay. At the outset, we proposed that there are regional and temporal differences or patterns in growth and mortality rates of bay anchovy larvae in Chesapeake Bay. To test this hypothesis, we analyzed otolith microstructure to estimate and compare month-specific (June vs. July), and region-specific (three regions) growth and mortality rates. Increments are deposited daily on sagittal otoliths of bay anchovy, providing a record of age (Fives et al., 1986; Leak and Houde, 1987; Castro and Cowen, 1991; Zastrow et al., 1991). Deposition of otolith increments begins on the third day after hatching and has been documented in laboratory experiments (Leak and Houde, 1987). Here, we discuss how regional or temporal variability in growth and mortality might influence potential for recruitment and production. We compared growth and mortality rates of bay anchovy larvae in relation to abundances of gelatinous predators and zooplankton (larval prey), and in relation to salinity and temperature. Overall, our objective was to determine which region(s) of the Bay and what part of the spawning season contributed most to survival and subsequent production of bay anchovy early-life stages.

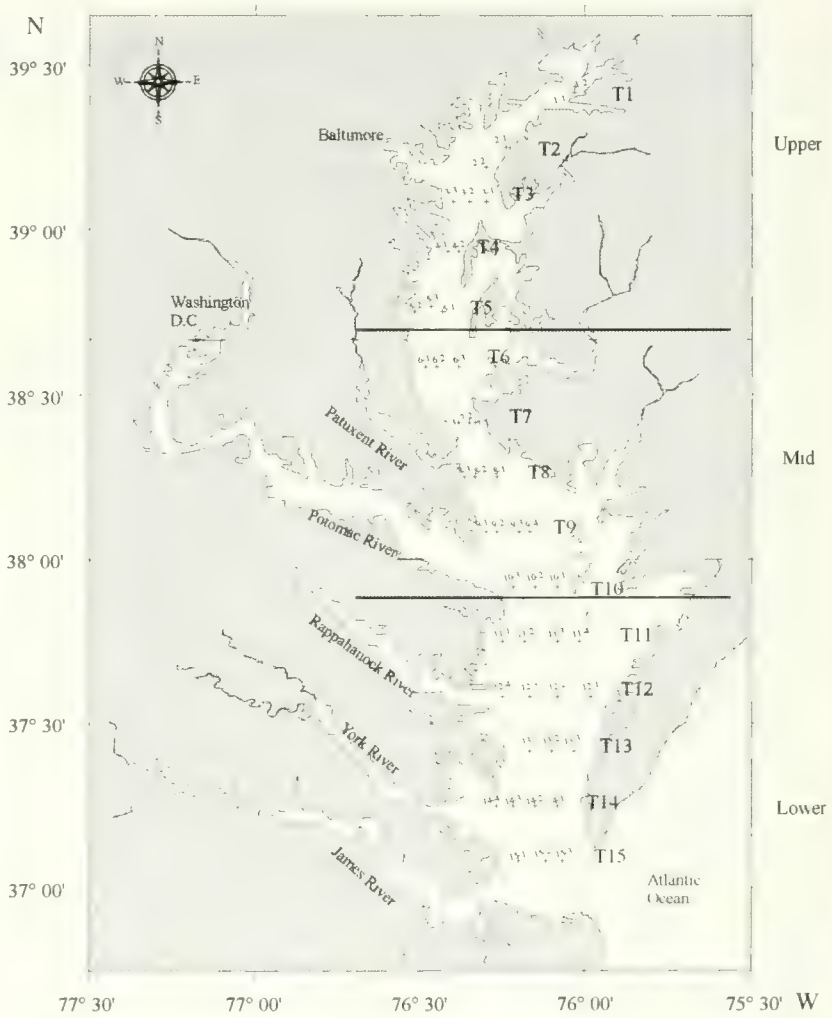

Figure 1

Chesapeake Bay. Regions, transects, and station locations for ichthyoplankton samples, zooplankton samples, and CTD casts, 19–22 June and 23–30 July 1993.

Materials and methods

Ichthyoplankton was collected throughout Chesapeake Bay during two baywide cruises, 19–22 June and 23–30 July 1993 (Fig. 1). Forty-six stations were sampled in June and 48 in July. Stations were on 15 transects spaced at 18.5-km (10 nmi) intervals from

the head of the Bay (39°25'N) to near the Bay mouth (37°05'N). Data were analyzed and compared in three regions: upper bay—transects 1–5 (39°25'N–38°45'N); mid bay—transects 6–10 (38°45'N–37°55'N); and lower bay—transects 11–15 (37°55'N–37°05'N).

At each station, ichthyoplankton was collected in one net of an opening-closing, 60-cm bongo sampler with 280-μm meshes and preserved in ethanol. Two tows, of 2-min duration, were made at each station. The first tow was from within 1 m of bottom to the pycnocline, and the second was made from the pycnocline (or middepth when no pycnocline was present) to the surface. Sampling protocols and methods to estimate densities and abundances of organisms are detailed by Rilling and Houde, manuscript in review); only brief descriptions are given here.

Immediately before each tow, a conductivity-temperature-depth (CTD) cast was made from within 1.0 m of bottom to within 1.0 m of the surface to provide depth profiles of temperature, salinity, and dissolved oxygen. To make results comparable to those of Dorsey et al. (1996) and MacGregor and Houde (1996), temperature, salinity, and dissolved oxygen were examined at 3-m depth. Zooplankton from either three or four designated depths was sampled in 10-L Niskin bottles and collected on 35-μm mesh. Gelatinous zooplankters from each ichthyoplankton tow were counted and their biovolumes recorded.

In the laboratory, anchovy larvae were measured to the nearest 0.1 mm standard length (SL). Lengths were corrected for shrinkage during collection and preservation (Theilacker, 1980; Leak, 1986). Small larvae of bay anchovy may be extruded through net meshes (Leak and Houde, 1987). Therefore, we applied a regression method to adjust abundances of <5.5 mm SL larvae collected in the 280-μm net meshes. The regression, which adjusted abundances of larvae upward by factors of 2.3 (at 2.0 mm), 1.9 (at 3.0 mm), 1.6 (at 4.0 mm), and 1.2 (at 5.0 mm larvae), was derived from comparisons of length-specific abundances in paired tows of 53-μm and 280-μm mesh bongo nets made in Chesapeake Bay under conditions similar to those during this survey (MacGregor, 1994; Rilling and Houde, manuscript in review).

Otolith analysis

Otolith microstructure was analyzed to estimate age, growth, and mortality. In the present study, sagittal otoliths from 509 larvae were examined. Otoliths from representative samples of larvae from each region of the Bay were examined for each cruise. Each larva in the otolith analysis was measured to the nearest 0.1 mm SL. Otoliths from larvae of 2.0 to 25.0 mm SL were mounted in "Epon" under a cover slip, and heated for 24 h at 60°C to harden the epoxy (Secor et al., 1991). Otolith increments were counted on two separate occasions under a compound light microscope at 600 to 1000× magnification by one reader (Rilling). The mean of the two increment counts plus two days was the estimated age.

Growth rates

Growth in length of larvae (mm/d) was estimated from the slopes of the linear regressions of shrinkage-adjusted lengths (SL) on ages from daily otolith-increment analysis:

$$L_t = a + gt,$$

where L_t = standard length (mm) at age t (d);
t = age (d) = otolith increment count plus two days;
g = growth rate (mm/d); and
a = y-intercept, the estimated length (mm) SL at hatch.

Gompertz growth models (Bolz and Burns, 1996) also were fitted to the data for each region and cruise. The fits were no better than those for the linear model and were not considered further in our analysis.

Larval lengths were converted to dry weights (g) from a weight-length relationship:

$$W = 0.1550 \times L^{3.5307},$$

where W = dry weight (g); and
L = mm SL.

Rates of growth in weight then were estimated from an exponential model, fitted by regressing $\log_e$-transformed dry weights on age:

$$W_t = W_0 e^{Gt},$$

where W_t = dry weight (g) at age t (d);
W_0 = dry weight (g) at hatch (the y-intercept of the log-linear regression); and
G = weight-specific growth coefficient (/d).

Coefficients in growth-model regressions were compared among regions and between cruises (months) in analysis of covariance (ANCOVA). The ANCOVAs tested for differences in slopes (growth rates) and y-intercepts in the growth equations. When significant differences were found, a multiple range test (Student-Newman-Keuls) was applied to determine which of the growth rates differed significantly. The

mean baywide growth-in-length and growth-in-weight rates for each cruise were estimated from regressions fitted to pooled length and age data from all stations. Because larvae collected in June were ≤13 mm SL, growth rates of larvae collected in July were estimated from two separate regressions—one for larvae ≤13 mm SL that was directly comparable to the June data and one for larvae >13 mm SL.

Mortality rates

Age-length keys were developed to convert larval length distributions to age distributions from which mortality rates then were estimated. To derive the keys, linear regressions, based upon subsamples of otolith-aged larvae from each cruise and region, were fitted to larval age-on-length relationships. For each regression, the standard error of the estimated regression coefficient was used to calculate a standard normal deviate (z-statistic) from which probabilities of ages of larvae within 1.0-mm length classes were obtained. Six age-length keys were constructed, one for each region and cruise. This maintained the region-specific integrity of size-at-age data, allowing estimation of region-specific mortality rates.

Instantaneous daily mortality rates of larvae were estimated from an exponential model of decline in abundance with respect to age:

$$N_t = N_0 e^{-Mt},$$

where N_t = abundance (number/m^2) at age t (d);
N_0 = estimated initial abundance (y-intercept of regression; number/m^2);
M = instantaneous mortality coefficient (/d); and
t = age (d).

The data were fitted to the log-linear form of the model after $\log_e$-transformation of the abundance data.

Region-specific mortality coefficients were estimated and compared within each cruise by analysis of covariance (ANCOVA). Mean baywide mortality rates for each cruise (month) were estimated by pooling abundance-at-age data from all stations and then compared in ANCOVA. When significant, ANCOVAs were followed by a multiple comparison test (Student-Newman-Keuls) to determine which mortality estimates differed significantly. Two separate mortality rates were estimated for larvae collected in July—one for larvae ≤13 mm SL (<18-day-old larvae) that was directly comparable to the June data that included only larvae of those ages, and one for larvae >13 mm SL (≥18-day-old larvae). Length-specific mortality rates also were estimated, by regressing $\log_e$-transformed abundances of larvae on 1-mm length classes.

M/G ratio and stage-specific survivorship

Stage-specific survival can be estimated from the M/G ratio, where M is the instantaneous mortality rate, and G is the weight-specific growth coefficient. The M/G ratios were compared between cruises and among the three designated regions of Chesapeake Bay. The ratio M/G is an indicator of stage-specific survivorship and production potential of larval cohorts (Houde, 1996, 1997a, 1997b). The ratio, sometimes termed the "physiological mortality rate," expresses a population's mortality per unit of individual growth (Beyer, 1989).

Stage-specific survival of bay anchovy larval cohorts was estimated as

$$S = [W_s / W_0]^{-(M/G)},$$

where S = stage-specific survival = N_s/N_0;
N_s = number of survivors at the end of a stage;
N_0 = number alive at the beginning of a stage;
W_s = dry weight of a 12-mm-SL bay anchovy larva (1000 mg);
W_0 = dry weight of a 3-mm-SL bay anchovy larva (10 g). [Note: This weight is more accurate than weight estimated for a 3-mm larva from the weight-length relationship, which overestimated weights of the smallest larvae]; and
M/G = ratio of instantaneous mortality coefficient (M) and weight-specific growth coefficient (G).

Survival to 12 mm SL, the largest length class fully represented in collections in each of the months, was calculated for each region by multiplying stage-specific survival rate (S) by estimated abundance of the smallest fully represented length class (i.e. N_0 at 3 mm SL). Stage-specific survival rates also were estimated for egg to 3-day larva, 3-day to 10-day larva, and 10-day to 18-day larva. Age-specific production at a station was obtained by multiplying estimated larval density (number/m^3) by the volume represented by the station. Regional productions were obtained by summation of larval abundances for all stations in each region.

Correlations and predictions

Multiple regression analyses were applied to determine if bay anchovy larval growth and mortality

rates could be related to biological or environmental factors. The four independent variables considered for inclusion were gelatinous predator biovolume (mL/m^2), zooplankton density (number/L), temperature, and salinity. Mean regional estimates of independent variables were entered into the regression model. Prior to multiple regression analysis, simple correlation analyses were run to determine which independent variables might be colinear and unsuitable for inclusion in the multiple regression model (SAS Institute, 1990). Pairs of independent variables with a correlation coefficient >0.70 were considered highly correlated and thus excluded from the multiple regression analysis.

Zooplankton analyses

In the laboratory, zooplankton organisms were identified by using a dissecting microscope. Zooplankton that were potential prey of larval anchovy were enumerated, i.e. copepods, barnacle nauplii, gastropod veligers, bivalve veligers, cladocerans, rotifers, tintinnids, polychaete larvae, and chaetognaths. Copepods were categorized as adults, copepodites, and nauplii. Densities of zooplankters were calculated as

$$D = N/V,$$

where D = density of organisms (number per liter);
N = number of organisms in a 10-L Niskin-bottle sample; and
V = sample volume (10 liters).

Densities were weighted according to the depth range represented by each sample to obtain a weighted mean density in the entire water column:

$$\overline{D} = \frac{\sum_{i=1}^{k} D \times m}{\sum_{i=1}^{k} m},$$

where m = depth ranges represented by each Niskin-bottle sample; and
k = number of Niskin-bottle samples taken on a CTD cast (3 or 4).

Results

Hydrography

Mean temperatures, salinities, and oxygen levels at 3-m depth in Chesapeake Bay differed significantly between June and July 1993 (t-test, $P<0.0001$). In each month, there was a well established pycnocline. Baywide mean temperature increased from 25.3°C in June to 26.6°C in July. Mean salinity baywide increased from 10.1 psu in June to 15.9 psu in July (Table 1) and increased in both months between the upper and lower regions of the Bay (ANOVA, $P<0.001$). Mean dissolved oxygen levels decreased from 7.8 mg/L in June to 6.3 mg/L in July. In June, 3-m DO levels ranged from 4.1 to 12.6 mg/L ; in July they were lower, 4.6 to 8.4 mg/L. Hypoxic and near-anoxic conditions (≤2.0 mg O_2/L) were most prevalent in the deep channel of the mid bay region, especially in July.

Growth

Baywide, mean growth rate of anchovy larvae increased from 0.59 mm/d in June to 0.72 mm/d in July (ANCOVA, $P<0.001$) (Fig. 2). When the analysis included only larvae ≤13 mm SL, an even higher baywide growth rate was estimated in July (0.78 mm/d) than in June (0.59 mm/d) (ANCOVA, $P<0.001$). Estimated lengths at 15 days after hatching were 11.65 mm SL in June and 13.72 mm SL in July.

Growth rates did not differ significantly among regions in June or July (ANCOVA, $P>0.05$) (Fig. 3). The regional estimates of growth-in-length rates ranged from 0.53 mm/d in the lower bay during June to 0.78 mm/d in the upper bay in July. Although not significantly different, the highest regional growth rates for each month were in the upper bay. The

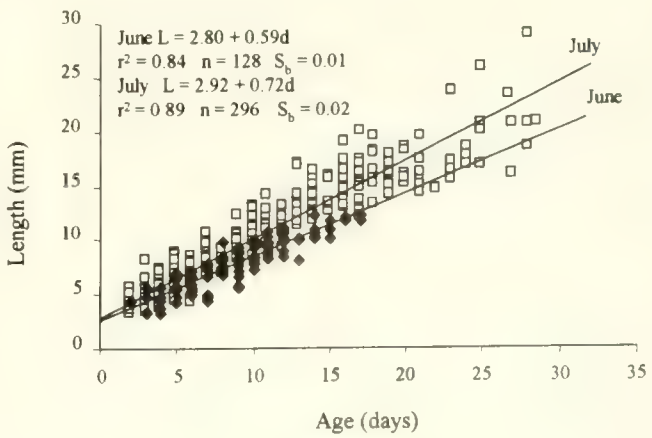

Figure 2

Baywide linear growth models for bay anchovy larvae in Chesapeake Bay, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis. ◆ = June, = July.

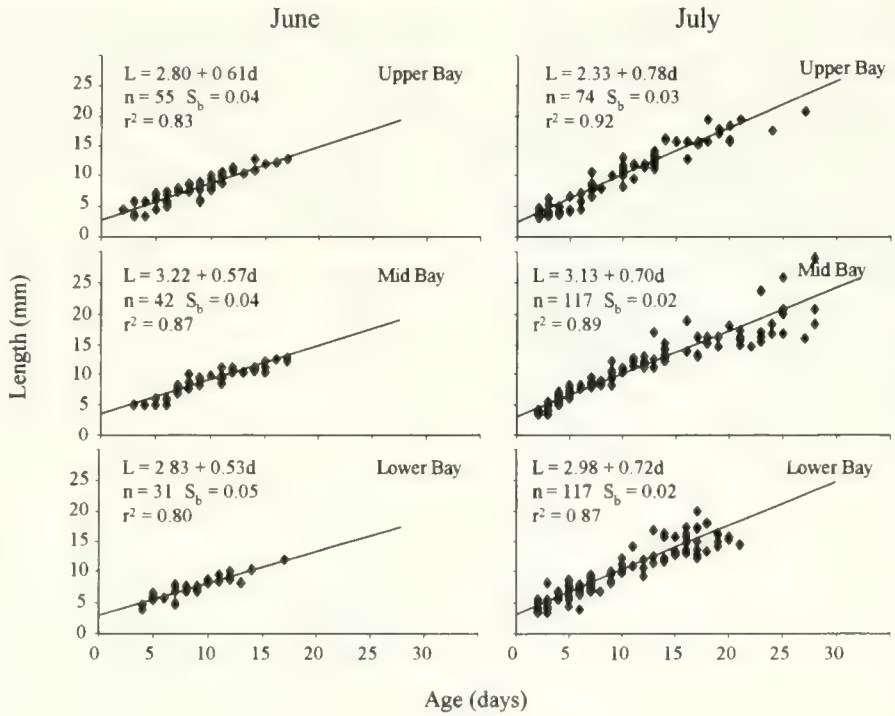

Figure 3

Linear growth models for bay anchovy larvae in upper, mid, and lower Chesapeake Bay regions, June and July 1993. L = standard length (mm), d = age in days, estimated from otolith-increment analysis.

y-intercepts of the linear regressions ranged from 2.33 mm to 3.22 mm and did not differ significantly among regions or between June and July (ANCOVA, $P>0.05$).

Growth in weight was rapid for surviving larvae. Baywide, estimated weight-specific growth rates G (/d) for larvae ≤13 mm SL (Table 1) increased from 0.26 in June (29.7%/d) to 0.35 in July (41.9%/d) (ANCOVA, $P<0.05$). For the ≤13 mm larvae, the highest regional G was 0.40 in the upper bay in July (49.2%/d), and the lowest G was 0.25 in the mid bay in June (28.4%/d). In July, an estimated baywide G for larvae >13 mm SL was only 0.11 (11.6%/d), a rate much lower than that of smaller larvae.

Mortality

Larvae experienced high mortality rates. Baywide instantaneous mortality coefficients M (/d) for larvae in all age classes declined significantly from 0.41 (33.6%/d) in June to 0.23 (20.5%/d) in July (ANCOVA, $P<0.0001$) (Fig. 4). When the data analysis included only larvae <18-days old (the oldest age represented in June) estimated July M = 0.22 (19.7%/d), a rate still significantly lower than the June rate (ANCOVA, $P<0.001$).

Larval mortality rates differed significantly among regions in June and July (ANCOVA, $P<0.0001$). Highest mortality rates in each month were in the lower bay. Regional daily rates ranged from 0.14 (13.1%/d) to 0.54 (41.7%/d) (Fig. 5). In June, the mid bay mortality rate was significantly lower than upper and lower bay rates. In July, when all regional mortality rates differed significantly, the lower bay had the highest mortality rate and the upper bay had the lowest rate (Student-Neumann-Keuls test).

Length-specific mortality rates (/mm) declined dramatically as larval length increased (Fig. 6). In June, the length-specific mortality rates ranged from 0.45/mm for 2–5 mm SL larvae to 0.07/mm for 10–13 mm SL larvae. In July, the rates were lower, ranging from 0.33/mm for 2–5 mm SL larvae to 0.05/mm for 10–13 mm SL larvae. The highest regional length-specific rate, 0.64/mm, occurred in the mid bay during July for the 2–5 mm SL class.

M/G ratio, production, and survival

The baywide M/G ratio declined from 1.59 in June to 0.67 in July (Fig. 7), indicating a nearly 70-fold higher survival and biomass production of cohorts

Table 1

Summarized data, Chesapeake Bay cruises, 19–22 June and 23–30 July 1993. Data include anchovy weight-specific growth rates (/d), mean biovolumes (mL/m^2) of gelatinous predators *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, mean densities (organisms/L) of zooplankton (ZOOP), mean regional temperatures (T) and salinities (S) at 3-m depth. Identical superscripts indicate no significant difference (P>0.05, Tukey's multiple range test) among regions or between months. SE = standard error.

Region	T (°C)	S (psu)	ZOOP (/L)	Vol. of *M. leidyi* (mL/m^2)	Vol. of *C. quinquecirrha* (mL/m^2)	Weight-specific growth rate G (/d)
June						
Upper bay	25.4^a	5.8^a	326.8^a	41.4^a	0.0^a	0.28^a
SE			116.7	22.1	—	0.01
Mid bay	25.3^a	9.7^b	23.1^b	999.5^b	0.0^a	0.25^a
SE			7.2	211.3	—	0.01
Lower bay	25.3^a	14.7c	68.6^b	516.8^a	0.0^a	0.25^a
SE			21.7	134.4	—	0.02
July						
Upper bay	26.8^a	8.9^a	442.5^a	229.6^a	30.7^a	0.40^a
SE			91.3	65.2	12.1	0.02
Mid bay	26.8^a	12.6^b	162.5^b	204.5^a	36.4^a	0.37^a
SE			35.5	44.7	7.9	0.03
Lower bay	26.2^a	26.2c	277.2^a	12.1^b	22.0^a	0.28^a
SE			40.0	7.2	11.8	0.02
Baywide						
June	25.3^a	10.1^a	138.5^a	560.7^a	0.0^a	0.26^a
SE			43.9	104.2	—	0.01
July	26.6^b	15.9^b	289.0^b	139.1^b	29.5^b	0.35^b
SE				27.4	6.1	

in the 3–12 mm SL size range during July. The increase in growth and decline in mortality rates between June and July accounted for the drops in M/G ratio. On average, larval cohorts lost biomass in June (M/G>1.0), but gained biomass in July (M/G <1.0). In June, cohorts at 12 mm SL supported only 6.6% of the biomass present at 3 mm SL, whereas, in July, cohorts at 12 mm SL supported 457.1% of their 3-mm-SL biomass. Each regional M/G ratio also declined between June and July.

Predicted abundance of larval daily cohorts at 12 mm SL, based upon the M/G ratios and estimated regional abundance-at-age data, was highest in the upper bay in June but shifted to the mid and lower bay in July (Table 2). Stage-specific mortality rates, estimated from declines in abundances, were highest for the youngest stages, and declined with increasing age (Table 3). In this analysis, abundances were estimated for cohorts at 18 days after hatching, when regional mean lengths ranged from 12.4 to 16.4 mm SL. Despite highest regional mortality, daily cohorts from the lower bay in July produced the most 18-day-old larvae (1.5×10^8). The daily production of 18-day-old larvae in the lower bay was 3.4–4.6 times higher than in other regions in July, and from 7 to 50 times higher than in other regions in June.

Cumulative mortalities from egg to 18-day old larval stage were lowest in the mid bay in June but lowest in the upper bay in July. Interestingly, those regions had experienced the greatest egg to 3-day-old larval mortalities, which then were followed by low mortality in older larvae (Table 3).

Predators and prey

There was a significant between-cruises difference in mean combined biovolumes of two common gelatinous predators of bay anchovy eggs and larvae, the ctenophore *Mnemiopsis leidyi*, and the scyphomedusa *Chrysaora quinquecirrha*, (t-test, P<0.001) (Table 1). Mean biovolumes of the ctenophore shifted regionally and declined by a factor of four in July. The scyphomedusan did not occur in June and had a mean biovolume of 29.5 mL/m^2 in July, and there was no indication of regional differences (ANOVA P>0.05) (Table 1).

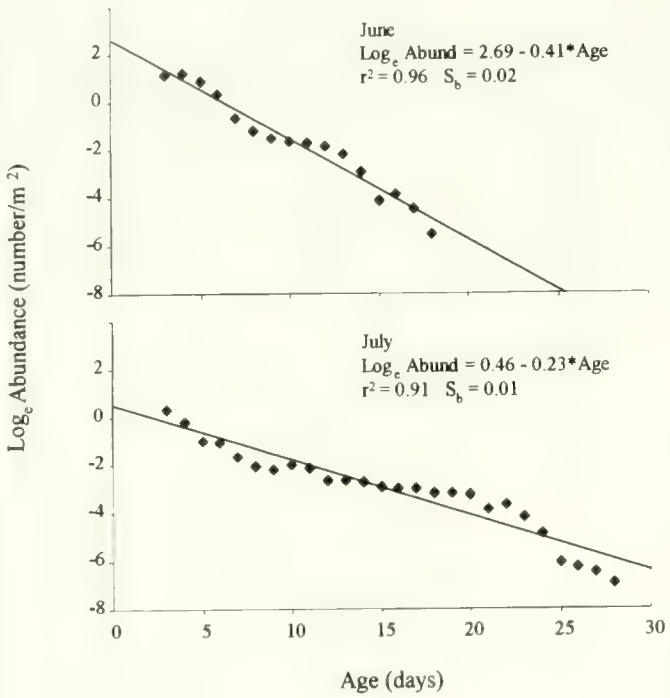

Figure 4

Age-specific survival curves for bay anchovy larvae in Chesapeake Bay, June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 2

Predicted cohort survivorships of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993. N_0 = estimated number of smallest fully represented length class of larvae (3 mm SL). M/G = ratio of instantaneous mortality rate (/d) to weight- specific growth rate (/d), survival rate (S) = $[W_s/W_0]^{-(M/G)}$ where W_s = dry weight of a 12-mm-SL larva (1000 μg), W_0 = dry weight of a 3-mm-SL larva (10 mg), and apparent survivorship at 12 mm = $S \times N_0$.

Region	N_0 (3-mm-SL larvae)	M/G	Survival rate	Apparent survivorship at 12 mm SL
June				
Upper bay	2.59×10^{10}	1.72	0.0004	1.04×10^{7}
Mid bay	2.49×10^{8}	0.87	0.0180	4.48×10^{6}
Lower bay	7.28×10^{7}	2.17	0.00005	3.64×10^{5}
July				
Upper bay	5.95×10^{8}	0.35	0.200	1.19×10^{8}
Mid bay	2.08×10^{10}	0.62	0.058	1.21×10^{9}
Lower bay	11.72×10^{10}	1.19	0.004	4.69×10^{8}

Baywide, the mean density of zooplankton that are potential prey of anchovy larvae doubled between June and July (t-test, $P<0.05$) (Table 1). Mean density of zooplankton was highest in the upper bay in June (ANOVA, $P<0.05$) and was higher in the upper and lower bay than in the mid bay in July (ANOVA, $P<0.05$). Nauplii of the copepod *Acartia tonsa* were the single most abundant zooplankter collected. Tintinnids, rotifers, and the cyclopoid copepod *Oithona* sp. also were common. Mean density of copepod nauplii, a major prey of bay anchovy larvae, increased from 36.9/L in June to 110.5/L in July (t-test, $P<0.05$).

Correlations

At the regional level, few correlations were judged to be significant at the $\alpha = 0.05$ level between biological and environmental variables (Table 4). The low degrees of freedom (n=6) and corresponding low power made it difficult to reject null hypotheses. Several coefficients were high enough to suggest possible correlations. Anchovy larval abundances were positively correlated with egg abundances (r=+0.96, $P<0.01$) and negatively correlated with gelatinous predator biovolumes (r=–0.87, $P<0.05$) (Fig. 8A). Larval growth rate was positively correlated with temperature (r=+0.94, $P<0.01$) (Fig. 8B) and possibly related to zooplankton density (r=+0.72, $P<0.11$). Although not significant at α = 0.05, anchovy egg abundances and zooplankton densities both may have been negatively correlated with gelatinous predator biovolumes (r =–0.76, P=0.08).

Predicting larval growth and mortality

Regional variability in anchovy larval growth-in-length rate for the combined June and July cruises was explained reasonably well by a two-variable regression model that included temperature and zooplankton density (r^2=0.93):

$$g = 0.32 + 0.05X_1 + 0.004X_2,$$

where g = larval growth rate (mm/d);
X_1 = $\log_e$ zooplankton density (organisms/L); and
X_2 = temperature (°C).

Larval growth rates increased with increasing temperatures and zooplankton densities. Temperature accounted for more of the variability in growth rate than did zooplankton density. Observed and model-

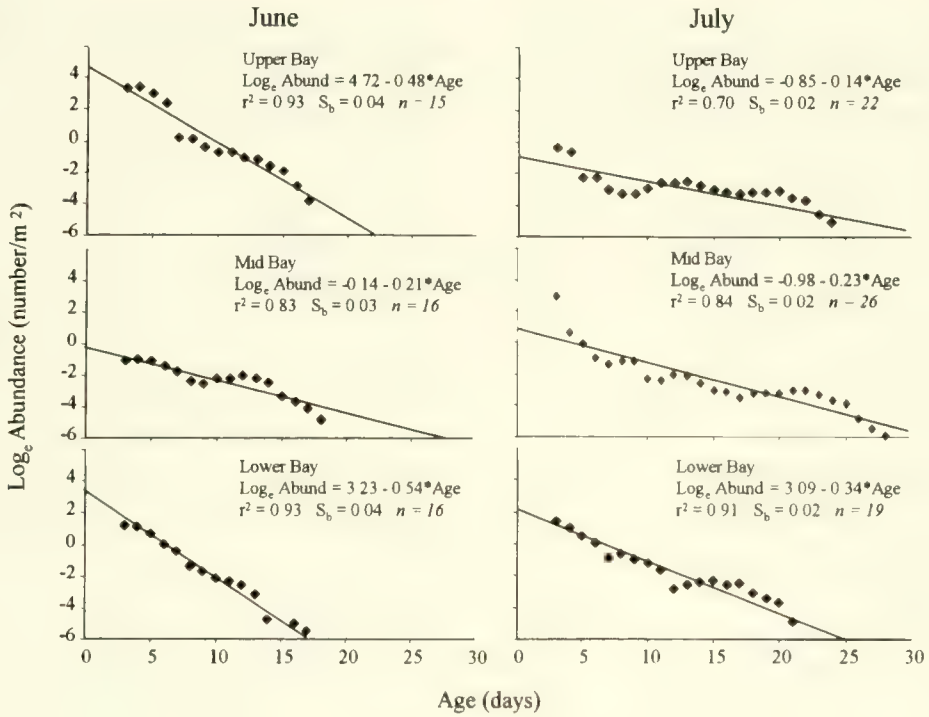

Figure 5

Age-specific survival curves for bay anchovy larvae in the upper, mid, and lower Chesapeake Bay regions in June and July 1993. The age-specific abundance estimates for each day class were derived from age-length keys.

Table 3

Estimated abundances, stage-specific mortality rates, and daily cohort production of bay anchovy larvae in the upper, mid, and lower Chesapeake Bay in June and July 1993, based upon declines in total numbers of larvae between stages. Stage A = estimated daily production of anchovy eggs by region. Stage B = estimated number of the smallest fully represented age class of larvae (3-d-old larvae). Stage C = estimated number of 10-day-old larvae. Stage D = estimated number of oldest represented age class of larvae (18-d-old larvae). Apparent loss rates for each stage, and cumulative mortalities also are given.

Region	Stage A (egg production)	Stage B (3-d old larvae)	Apparent loss rate A → B (M/d)	Stage C (10-d old larvae)	Apparent loss rate B → C (M/d)	Stage D (18-d old larvae)	Apparent loss rate C → D (M/d)	Cumulative mortality B → D	Apparent survival
June									
Upper	8.87×10^{11}	2.59×10^{10}	1.18	4.42×10^{8}	0.58	2.16×10^{7}	0.38	7.09	0.0008
Mid	10.44×10^{11}	2.49×10^{8}	2.78	1.06×10^{8}	0.12	6.52×10^{6}	0.35	3.64	0.0263
Lower	23.28×10^{11}	7.28×10^{9}	1.92	1.42×10^{8}	0.56	2.45×10^{6}	0.51	8.00	0.0003
July									
Upper	3.21×10^{11}	5.95×10^{8}	2.09	4.14×10^{7}	0.38	3.26×10^{7}	0.03	2.90	0.055
Mid	1.53×10^{12}	2.08×10^{10}	1.43	1.33×10^{8}	0.72	4.39×10^{7}	0.14	6.16	0.002
Lower	6.58×10^{12}	11.72×10^{10}	1.34	9.29×10^{8}	0.69	1.50×10^{8}	0.22	6.66	0.001

predicted values of mean regional larval growth rates differed by no more than 6%. No satisfactory multiple regression model could be fit for larval mortality.

Discussion

Cohorts of bay anchovy larvae in Chesapeake Bay do not experience uniform growth and mortality.

Growth rates were temporally variable, and mortality rates were both spatially and temporally variable. It was clear that variability in these rates could significantly alter production and recruitment potentials. Baywide, larval growth rates were higher in July than in June. The larval growth rates that we report are higher and more variable than rates reported previously for bay anchovy in the laboratory and in most field studies (Table 5). Gallagher et al. (1983) did report equivalent and higher growth rates (0.59–0.93 mm/d) in the Patuxent River tributary of Chesapeake Bay.

Temporal and spatial variability in anchovy larval growth rates was related to both zooplankton density and temperature. The mean baywide growth rate of larvae increased from 0.59 mm/d in June to 0.72 mm/d in July, corresponding to increases in mean water temperatures and mean copepod nauplii densities. The increase in larval growth rate between months corresponded to a coincident 1.3°C increase in mean temperature at 3-m depth and to a major increase in zooplankton abundance. On the basis of laboratory experiments, Houde (1978) predicted minimal prey concentration for 10% survival of bay anchovy larvae at 26°C to be 107 copepod nau-

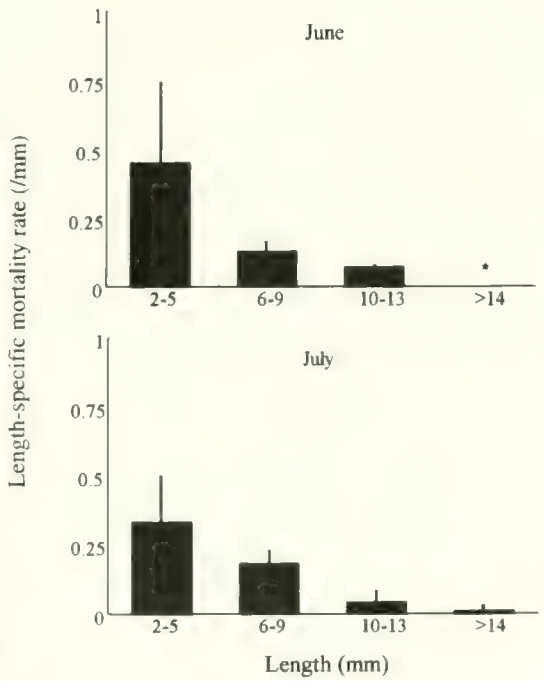

Figure 6

Baywide mean length-specific mortality rates (/mm) of bay anchovy larvae in four length classes during June and July 1993. Error bars are ±1 SE. * = no data.

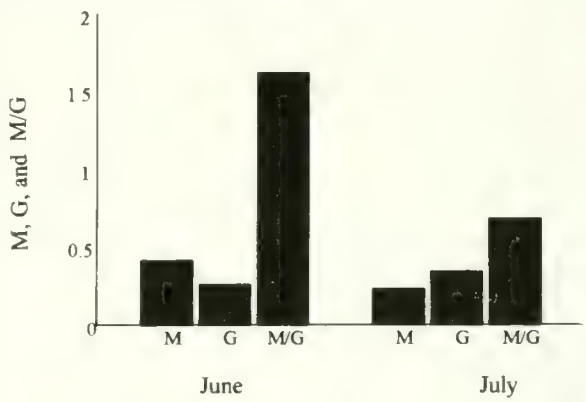

Figure 7

Baywide daily instantaneous mortality rate (M), weight-specific growth rate (G), and M/G ratios for bay anchovy larvae in Chesapeake Bay, June and July 1993.

Table 4

Correlation coefficients at the regional level (n=6) for data collected in Chesapeake Bay, June and July 1993. The seven variables include mean regional instantaneous larval mortality rate (M, /d), larval growth rate (g, mm/d), egg and larval abundances (number/m^2), $\log_e$-combined gelatinous predator biovolumes (mL/m^2) of *Mnemiopsis leidyi* and *Chrysaora quinquecirrha*, zooplankton density (organisms/L), and temperature and salinity at 3-m depth. * = $P<0.05$, ** = $P<0.01$. In each case, $n = 6$, $r_{.05,4} = 0.81$.

	M	g	Egg abundance	Larval abundance	Jelly biovolume	Zooplankton density	Temperature (°C)
g	−0.685						
Egg abundance	0.364	0.056					
Larval abundance	0.434	0.165	0.955**				
Jelly biovolume	−0.287	−0.380	−0.765	−0.868*			
Zooplankton density	−0.039	0.721	0.251	0.477	−0.761		
Temperature	−0.771	0.938**	−0.027	0.037	−0.170	0.555	
Salinity	0.111	0.091	0.524	0.521	−0.132	−0.072	0.067

plii/L. In the present study, nauplii densities often exceeded that level in July, but levels were lower and potentially limiting during June, especially in the mid bay (mean=9.7 nauplii/L) and lower bay (mean=17.7 nauplii/L).

During each month, fastest growth rates were estimated for larvae from the upper bay where copepod nauplii were most abundant (means=84.8 nauplii/L in June and 157.5 nauplii/L in July). Lowest growth was estimated during June in the mid and lower bay, where copepod nauplii densities and mean temperatures were lowest. Although temperature alone may exercise an important control over larval growth, (Houde, 1989a; Pepin, 1991), a combination of factors, including prey availability, effects of body size, or growth-rate dependent mortality, may operate to control growth rates and survival potential (Bailey and Houde, 1989; Heath, 1992; Leggett and DeBlois, 1994). In the case of bay anchovy, all of these factors may operate, but temperature and prey level apparently predominate. There also was an effect of body size; growth rate of larvae >13 mm declined. In a synthesis analysis, Houde (1997b) reported that average weight-specific growth coefficients of bay anchovy declined progressively from 0.573 (77.3%/d) in newly hatched larvae to 0.065 (6.7%/d) in near-metamorphosis individuals.

Our baywide instantaneous daily mortality rates decreased from 0.41 in June to 0.23 in July 1993. This decline was coincident with increasing growth rate, suggesting that cohorts of rapidly growing larvae in July might have been less vulnerable to size-selective or growth-rate dependent predation. From length-specific and age-specific analyses of mortality, it was clear that mortality rates were greatest for the smallest and youngest larvae (Table 3). Houde (1997b), analyzed the accumulated data on bay anchovy larvae from Chesapeake Bay and demonstrated that mortality rate (M) declined predictably with respect to body weight raised to the –0.318 power. In the present study, mortality from the egg to 3-day-old larval stage was 2 to 7 times higher than mortality from the 3- to 10-day-old larval stage. Interestingly, mean baywide mortality rates for the egg to 3-day-old stage (yolksac and first-feeding larvae) were similar in June and July (82%/d in June, 79%/d in July), but mortality rates for the 10 to 18-day-old larval stage were considerably lower in July (34%/d in June, 12%/d in July), implying that conditions had become more favorable for feeding-stage larvae in July. Baywide cumulative mortality rates for egg to 18-day-old larvae indicated that <0.1% of a daily cohort survived to 18 days after hatching in June and that ~1.6% survived to 18 days in July.

Predation is a major cause of mortality in the early life of marine fishes (Leggett, 1986; Bailey and Houde, 1989; Leggett and DeBlois, 1994) and may

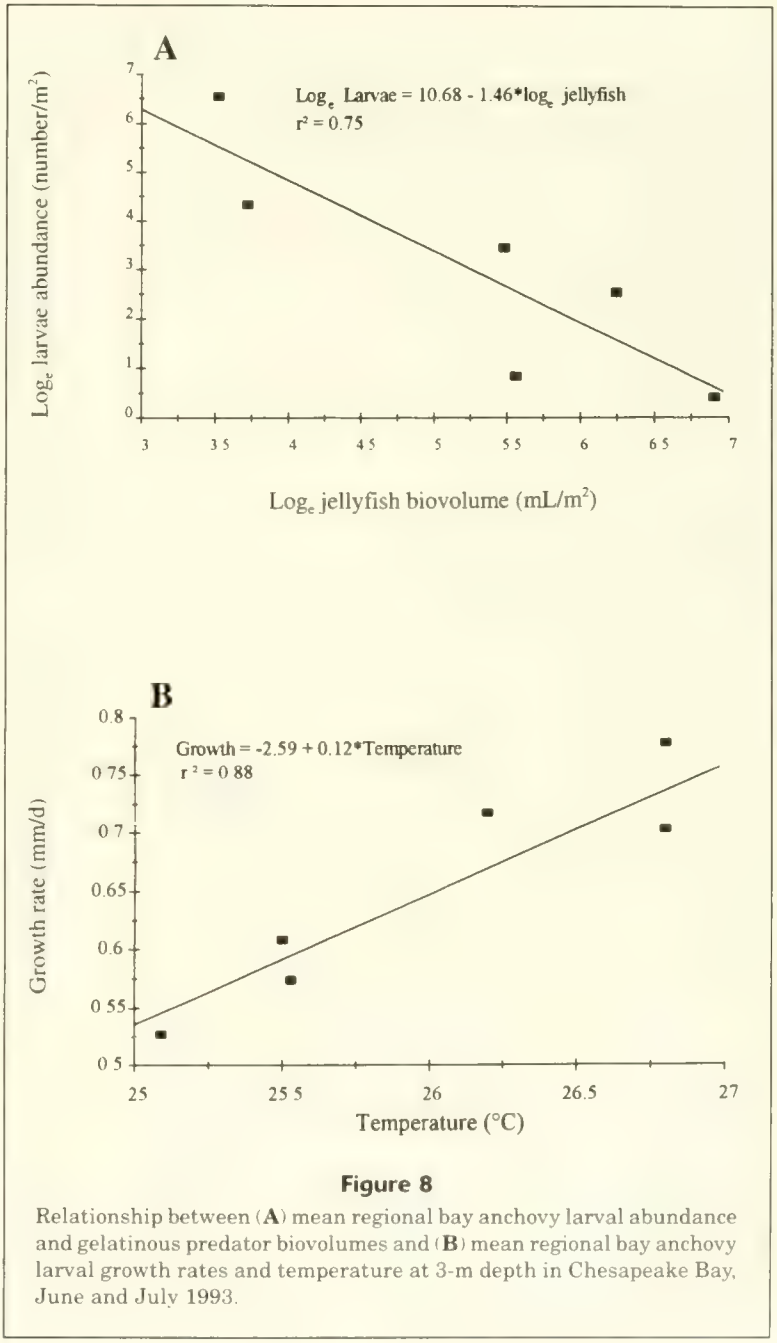

Figure 8

Relationship between (**A**) mean regional bay anchovy larval abundance and gelatinous predator biovolumes and (**B**) mean regional bay anchovy larval growth rates and temperature at 3-m depth in Chesapeake Bay, June and July 1993.

Table 5

Reported growth and mortality rates of bay anchovy larvae in field studies.

Location	Growth (mm/d)	Mortality (M/d)	Source
Patuxent River, MD	0.59–0.93		Gallagher et al. (1983)
Newport River Estuary, NC	0.25–0.51		Fives et al. (1986)
Biscayne Bay, FL	0.43–0.56	0.30–0.45	Leak and Houde (1987)
Mesocosms in Chesapeake Bay, MD	0.39–0.61	0.08–0.23	Cowan and Houde (1990)
Great South Bay, NY	0.52–0.59	0.32–0.89	Castro and Cowen (1991)
Chesapeake Bay, MD (yolksac larvae)		0.41–4.24	Dorsey et al. (1996)
Chesapeake Bay, MD		0.23–1.20	MacGregor and Houde (1996)
Chesapeake Bay, MD	0.53–0.78	0.14–0.54	This study, range of regional rates

be the major agent of mortality operating on bay anchovy in Chesapeake Bay. The gelatinous zooplankters *M. leidyi* and *C. quinquecirrha,* are known to be important predators on eggs and larvae of bay anchovy (Feigenbaum and Kelly, 1984; Monteleone and Duguay, 1988; Cowan and Houde, 1993; Purcell et al., 1994). In Chesapeake Bay, the peak periods of bay anchovy spawning and gelatinous zooplankton abundance overlap during June and July (Cowan and Houde, 1993; Purcell et al., 1994), facilitating the predator-prey interaction. We found gelatinous predator biovolumes to be significantly higher in June, when only *M. leidyi* was present, than in July when both species occurred. *Chrysaora quinquecirrha*, a potentially more powerful predator on anchovy eggs and larvae than *M. leidyi* (Purcell et al., 1994), occurred only in July, but at low mean biovolumes that were uniform in the three Bay regions. It is worth noting that *C. quinquecirrha* is also a predator on *M. leidyi* (Purcell and Cowan, 1995), resulting in a predator-prey interaction that potentially has a sparing effect on anchovy eggs and larvae (Cowan and Houde, 1992).

The large biovolumes of gelatinous predators probably contributed to the greater mortality rates in June compared with July. However, the six mortality coefficients from the regional estimates were not significantly correlated with gelatinous predator biovolumes (Table 4), despite the strong, negative, linear relationship between anchovy larval abundance and gelatinous predator biovolume (r^2=0.75; Fig. 8A) for the combined June and July regional data. This negative correlation may have been a consequence of predation, but it also could have been generated by lower egg production of anchovy in areas where jellyfish were abundant, as Dorsey et al. (1996) hypothesized in site-specific studies of bay anchovy egg and yolksac larval mortality. Although we cannot conclude unequivocally that gelatinous predators accounted for high mortality rates, it is likely that they were significant consumers of anchovy larvae.

Abundance data illustrated in survival curves (Figs. 4 and 5) showed several modes, which suggested that cohort-specific mortality might be variable on shorter time scales than we studied and might be changing as a function of ontogeny, age, or size. Other factors also could have biased our mortality estimates or contributed to regional variability in rates, for example, pulses of spawning that produce variable initial abundances of daily cohorts or immigration and emigration of larvae into and out of a region. Because mortality is size-specific, the presence of larger larvae in July could have led to a lower estimate of mortality rate during that period. But, when only larvae of equivalent lengths (i.e. ≤13 mm SL) were analyzed, estimated mortality rates remained nearly twice as high in June (M=0.41) as in July (M=0.22). If some larvae were being advected up the bay, as Dovel (1971) had hypothesized, this process could have contributed to biased estimates of higher mortality rates in the lower bay.

Despite a high cumulative mortality rate, the lower bay in July had the highest production of larvae surviving to 18 days after hatching for the June–July 1993 period (Table 3). This result is due to high spawning activity and initial concentrations of larvae in the lower bay (Rilling and Houde, manuscript in review), a high growth rate of larvae, and, importantly, the relatively large volume of water in the lower bay, which supported a large contingent of anchovy larvae.

Survival and recruitment potential of anchovy cohorts were responsive to variability in both mortality rates and growth rates that they experienced. The ratio M/G, an index of stage-specific mortality, is an important indicator of comparative production and survival potential during early life (Houde, 1996,

1997a). The baywide M/G ratio for bay anchovy larvae declined from 1.59 in June to 0.67 in July. The low M/G ratio in July is a reflection of the coincident decline in larval mortality rate and increase in growth rate that occurred between June and July. The difference in M/G ratios between months implies a 70-fold higher survival potential through the larval stage for July-hatched cohorts.

M/G ratios <1.0, signifying high regional production potential, were observed in the mid bay in June and in the mid and upper bay in July. Larvae in those regions tended to have lowest mortality rates. An abundance of large larvae generally indicates higher survival rates of cohorts, but size-selective mortality or transport (or both) of larvae into a region (Fortier and Leggett, 1982, 1985; Norcross and Shaw, 1984; Boehlert and Mundy, 1988) could have contributed to the relative abundances of large larvae and low M/G ratios. In the Patuxent River subestuary of Chesapeake Bay, progressive increases in larval length upriver were reported by Loos and Perry (1991), who hypothesized (with supporting evidence) that transport of larvae was primarily responsible. Similarly, MacGregor and Houde (1996) reported a gradient in bay anchovy larval size on a cross-Bay transect that was repetitively sampled; smallest larvae were found offshore and largest larvae, inshore. In the present study, selective up-bay transport of larvae could have acted to reduce the M/G ratio in the upper bay between June and July, but we cannot confirm it.

In summary, mortality rates of bay anchovy early-life stages were both temporally and regionally variable at one-month temporal and at 60-km spatial scales in Chesapeake Bay. Growth rates showed strong temporal variation but no significant regional differences. Stage-specific survival, which depended upon both mortality and growth rates, was both size-specific and growth-rate dependent. We found no obvious indication of density-dependent mortality (i.e. no correlations between egg or larval abundances and mortality or growth rates), although recent individual-based modeling suggests that density-dependence in early-life could be an important regulator of bay anchovy recruitments in Chesapeake Bay (Wang et al., 1997). The lower Chesapeake Bay in July was the major source of potential recruits in 1993. Temperature, zooplankton prey, and gelatinous predators all are believed to have contributed to temporal and regional differences in growth and mortality of larvae. Further research is needed to define scales and patterns of processes that control variability in production and recruitment of bay anchovy. This will require coupled biophysical studies and development of models that, up to now, have essentially emphasized only biology.

Acknowledgments

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Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures

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Abstract.—Size at 50% maturity is commonly evaluated for wild populations, but the uncertainty involved in such computation has been frequently overlooked in the application to marine fisheries. Here we evaluate three procedures to obtain a confidence interval for size at 50% maturity, and in general for P% maturity: Fieller's analytical method, nonparametric bootstrap, and a Monte Carlo algorithm. The three methods are compared in estimating size at 50% maturity ($l_{50\%}$) by using simulated data from an age-structured population, with von Bertalanffy growth and constant natural mortality, for sample sizes of 500 to 10,000 individuals. Performance was assessed by using four criteria: 1) the proportion of times that the confidence interval did contain the true and known size at 50% maturity, 2) bias in estimating $l_{50\%}$, 3) length and 4) shape of the confidence interval around $l_{50\%}$. Judging from criteria 2–4, the three methods performed equally well, but in criterion 1, the Monte Carlo method outperformed the bootstrap and Fieller methods with a frequency remaining very close to the nominal 95% at all sample sizes. The Monte Carlo method was also robust to variations in natural mortality rate (M), although with lengthier and more asymmetric confidence intervals as M increased. This method was applied to two sets of real data. First, we used data from the squat lobster *Pleuroncodes monodon* with several levels of proportion mature, so that a confidence interval for the whole maturity curve could be outlined. Second, we compared two samples of the anchovy *Engraulis ringens* from different localities in central Chile to test the hypothesis that they differed in size at 50% maturity and concluded that they were not statistically different.

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Size at 50% maturity ($l_{50\%}$) is commonly evaluated for wild populations as a point of biological reference (see Table 1). To estimate $l_{50\%}$, a sample of organisms known to have just reached sexual maturity could be available and their arithmetic mean size can be used as an estimator. However, the sample needed to obtain such a design-based estimator (Smith, 1990) for wild populations might be too expensive and would involve time-consuming histological procedures. Fisheries biologists prefer to conceive size at first maturity as the average size at which 50% of the individuals are mature. With this conception, the estimator is not based on a sampling design but on a model of the relation between body size and the number of individuals that are mature from a total number at each of many size intervals. The variance of a design-based estimator is determined by sampling design (Thompson, 1992). The variance of a model-based estimator is not as easily obtained. A sample of published works in the fisheries literature provides a measure of the frequency with which statistical uncertainty of the model-based $l_{50\%}$ is ignored (Table 1). In this work, we show three alternative procedures: an analytical method derived from generalized linear models (McCullagh and Nelder, 1989), nonparametric bootstrap (Efron and Tibshirani, 1993), and a Monte Carlo algorithm developed in our study. We show by simulation the behavior of the three methods for sample sizes of 500 to 10,000 individuals, concluding that they are similar in terms of bias, length, and shape of confidence intervals but that the Monte Carlo method outperforms the other two methods in percentage of times that the confidence interval contains the true parameter, which remained close to the nominal 95% at all sample sizes.

The problem

In regression analysis, we are usually interested in assigning confidence bounds to the response variable at specified levels of the predictor variable. However, in maturity modeling the attention is turned to the converse problem of

Table 1

An example of published analyses on size at maturity in crustacean and fish populations. CW = carapace width; CL = carapace length; TL = total length; m = males; f = females; [g] = gonadal maturity; [m] = morphometric maturity.

Paper	Species	Fitting method	$l_{50\%}$ (mm)	CI 95%	CI estimation method
Somerton (1980)	*Paralithodes camtschatica*	Weighted nonlinear least-squares	102.8 (CL, m)	Not reported	Random partition of data into subsets and computation of var ($l_{50\%}$) among the N independent estimates of l_{50}
			101.9 (CL, f)	Not reported	
	Chionoecetes bairdi		114.7 (CW, m)	Not reported	
Campbell and Robinson (1983)	*Homarus americanus*	Nonlinear least-squares	108.1 (CL, f)	—	—
			92.5 (CL, f)	—	—
			78.5 (CL, f)	—	—
Somerton and MacIntosh (1983)	*Paralithodes platypus*	Weighted nonlinear least-squares	80.6 (CL, f)	79.4–82.6	Random partition of data into subsets and computation of var ($l_{50\%}$) among the N independent estimates of l_{50}
			96.3 (CL, f)	95.7–96.9	
			93.7 (CL, f)	92.9–94.5	
			87.4 (CL, f)	86.4–88.4	
Campbell and Eagles (1983)	*Cancer irroratus*	Nonlinear least-squares	62.0 (CW, m)	—	—
			49.0 (CL, f)	—	—
Somerton and Otto (1986)	*Lithodes aequispina*	Weighted nonlinear least-squares	97.7 (CL, f)	Values not reported	Bootstrap samples were drawn from the original data set for obtaining independent estimates of $l_{50\%}$, and then computing var($l_{50\%}$) among them.
			99.0 (CL, f)		
			110.7 (CL, f)		
			92.0 (CL, m)		
			107.0 (CL, m)		
			130.0 (CL, f)		
Gaertner and Laloé (1986)	*Geryon maritae*	Nonlinear least-squares	82.8 (CL, f)	—	Confidence regions for the parameters of a logistic function were computed.
Comeau and Conan (1992)	*Chionoecetes opilio*	Nonlinear least-squares	34.2 (CW, m)	—	—
Armstrong et al. (1982)	*Lophius americanus* (Pisces: Lophiiformes)	Linear regression of Prop. Mature (arcsine-square root transformed) on Total Length	368.9 (TL, m)	—	—
			458.3 (TL, f)	—	—
Lovrich and Vinuesa (1993)	*Paralomis granulosa*	Probit	50.2 (CL, m)[g]	—	—
			60.6 (CL, f)[g]	58.3–62.9	Not reported
			57.0 (CL, m)[m]	53.9–60.1	Not reported
			66.5 (CL, f)	63.4–69.5	Not reported
Roa (1993a)	*Pleuroncodes monodon*	Maximum likelihood	27.2 (CL, f)	24.2–30.2	Ratio of parameter estimates confidence limits
González-Gurriarán and Freire (1994)	*Necora puber*	Maximum likelihood	54.8 (CW, m)[g]	—	—
			49.8 (CW, f)[g]	—	—
			53.3 (CW, m)[m]	—	—
			52.3 (CW, f)[m]	—	—

setting a confidence interval for the size at which a fixed proportion of individuals in a population are sexually mature. That is, we need a procedure for estimating uncertainty in the predictor variable because management decisions are framed in terms of body size, and hence the uncertainty in estimation

must be transferred to this variable. The first part of the problem is the selection of the maturity model. The available data consist of size (normally length) and maturity status, which will be assumed to take only two values: mature or immature. The predictor variable is continuous and the response variable is dichotomous. With such variables, model errors distribute binomially. Welch and Foucher (1988) recognized this aspect of modeling maturity and showed an efficient procedure based on the principle of maximum likelihood that takes advantage of the binomial nature of the errors.

For dichotomous data modeled as a function of a continuous variable, the following simple logistic function is a consequence of the assumption of a linear relationship between the logit link function and a single predictor variable (Shanubhogue and Gore, 1987; Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989):

$$P(l) = \frac{\alpha}{1 + e^{\beta_0 + \beta_1 l}}, \quad (1)$$

where $P(l)$ = proportion mature at size l; and
α, β_0, and β_1 = asymptote, intercept, and slope parameters, respectively (see also Eq. 3).

The estimates of these parameters, given a data set, are chosen from the point at which the product of binomial mass functions of all data points (the likelihood of the data under the model) is a maximum, or equivalently when the negative of the log likelihood

$$-\ell(\alpha, \beta_0, \beta_1) = -\sum_l \left[(h_l) \ln(P(l)) + (n_l - h_l) \ln(1 - P(l)) \right] \quad (2)$$

is a minimum,

where h = the number of mature individuals; and
n = sample size at l;
$P(l)$ = Eq. 1; and

where a constant term that does not affect the estimation is omitted.

Given the nonlinear nature of normal equations, the minimum is found by an iteration algorithm. The parameters estimated by minimizing Equation 2 are maximum likelihood estimates (MLE). In practical situations, the logistic model may be modified from its original form to allow more biological reality (Welch and Foucher, 1988).

The result from fitting the model (Eq. 1) to the data by using the objective in Equation 2, is a vector of parameter estimates and a covariance matrix, which represents the uncertainty associated to them. With these results, we may undertake the converse problem of estimating size at fixed $P\%$ maturity, which takes the form

$$l_{P\%} = \frac{1}{\beta_1} \ln\left[\frac{1}{P} - 1\right] - \frac{\beta_0}{\beta_1}. \quad (3)$$

In Equation 3 it is assumed that the asymptote parameter (α) from Equation 1 is fixed at 1. This assumption is justified on the basis of several published works on size at maturity, showing that all individuals were mature above a given size during the reproductive season (Table 1). Furthermore, if $\hat{\beta}_0$ and $\hat{\beta}_1$ are MLE of β_0 and β_1 and they are used to compute $l_{P\%}$ from Equation 3, then $\hat{l}_{\%}$ is also MLE. We show below three procedures to perform this task and then test them by generating data from Monte Carlo simulation of the age-size structure and maturity progression of individuals of a hypothetical population.

Analytical estimation

The logistic model in Equation 1 belongs to a class of generalized linear models studied by McCullagh and Nelder (1989). These authors consider the problem of building approximate confidence intervals for the level of the predictor variable that gives rise to a fixed proportion in the response variable. They suggest the use of Fieller's (1944) theorem, according to which the linear combination

$$\beta_0 + \beta_1 l_{P\%} - g(P_0) = 0, \quad (4)$$

where $l_{P\%}$ = the value of the predictor variable for a fixed proportion; and $g(P_0)=ln(P_0/(1-P_0))$ (the logit link function) is approximately normal with mean zero and analytical variance given by

$$v^2(l_{P\%}) = \mathrm{var}(\hat{\beta}_0) + 2 l_{P\%} \mathrm{cov}(\hat{\beta}_0, \hat{\beta}_1) + l_{P\%}^2 \mathrm{var}(\hat{\beta}_1). \quad (5)$$

The $100(1-\alpha)\%$ confidence interval is the set of values defined by

$$\frac{1}{\hat{\beta}_1}\left(-\hat{\beta}_0 + g(P_0) \pm z_{\alpha/2} v(l_{P\%})\right), \quad (6)$$

where $z_{\alpha/2}$ = a quantile of the normal distribution.

Other link functions like probit, common in the field of toxicology (Finney, 1977), are not investigated in this paper.

Bootstrap estimation

Bootstrap is not a uniquely defined concept (Efron and Tibshirani, 1993). This means that bootstrap

samples may be obtained by conceptually different resampling procedures. In the context of logistic regression, it is possible to resample the observational pair (l_i,h_i), or the semiobservational pair $(l_i, P(l)+\varepsilon_i)$, with ε_i as a realization from the residual distribution of the logistic model. To be valid, this second resampling unit needs the assumption of independence between ε_i and l_i. As stated by Efron and Tibshirani (1993), this is a strong assumption that can fail even when the model $P(l)$ is correct. These authors remark that bootstrapping the observational pair is less sensitive to assumptions than bootstrapping residuals. Therefore, in our work an observation to be resampled with replacement is defined as the pair (length, maturity status). For each and all bootstrap samples, a resampled frequency distribution for $l_{P\%}$ is obtained by fitting the maturity model in Equation 1 with the objective function in Equation 2 and by computing $l_{P\%}$ with Equation 3. The confidence interval is obtained by application of the bias-corrected and accelerated (BCa) method, recommended by Efron and Tibshirani (1993).

Monte Carlo estimation

In Monte Carlo resampling, a model is assumed for the distribution of the estimator and then data are generated computationally to assess the amount of variation (Manly, 1997). In our case, we consider a Monte Carlo resampling of maturity parameters from the modeled joint probability distribution of the estimates $\hat{\beta}_0$ and $\hat{\beta}_1$ for computing $\hat{l}_{p\%}$ from Equation 3. In contrast to the bootstrap approach, the implementation of this approach needs only one fitting of the logistic maturity model and then uses the asymptotic distribution of estimated parameters of the model to generate the probability distribution of the derived statistic $l_{P\%}$. These parameter estimates, $\hat{\beta}_0$ and $\hat{\beta}_1$, distribute asymptotically bivariate normal, with mean vector equal to the population parameters and variance given by their covariance matrix (for nonlinear least-squares: Johansen, 1984; for maximum-likelihood estimates: Chambers, 1977). The bivariate normal distribution of $\hat{\beta}_0$ and $\hat{\beta}_1$ has a strong covariance component, which is the same as to say that these estimates are highly correlated. This also means that much of the variance in one estimate is given by the variance in the other one. Ignoring such correlation would lead to an overestimation of the variance of $l_{P\%}$. In a Monte Carlo setting, the correlation between parameter estimates may be considered in the computation by making the resampling of one estimate conditional on the resampling of the other one. In this work we develop such a technique using the theory of least-squares estimates of two linearly related normal variates (Draper and Smith, 1981). This approach is justified by the asymptotic nature of standard errors. If $\hat{\beta}_0$ and $\hat{\beta}_1$ and are two normal random variables that are linearly related, then we may write the linear equation

$$\hat{\beta}_1 = \hat{b}_0 + \hat{b}_1\hat{\beta}_0. \tag{7}$$

This equation may be reversed by writing $\hat{\beta}_0$ as a linear function of $\hat{\beta}_1$ because both are random variables. It can be shown that (Draper and Smith, 1981)

$$\hat{b}_1 = \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right], \tag{8}$$

where r is the estimated linear correlation coefficient between $\hat{\beta}_0$ and $\hat{\beta}_1$, and $S_{\hat{\beta}_0}$ and $S_{\hat{\beta}_1}$ are the respective standard errors. Furthermore, from Equation 7

$$\hat{b}_0 = \hat{\beta}_1 - \hat{b}_1\hat{\beta}_0. \tag{9}$$

Therefore, the high correlation coefficient between both maturity parameters can be accounted for by free sampling from the marginal distribution of one parameter estimate (for example, $\hat{\beta}_0$) in each Monte Carlo trial and by computing the other by using

$$\begin{aligned}\beta_{1,j} &= \hat{\beta}_1 - \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\hat{\beta}_0 + \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\beta_{0,j} \\ &= \hat{\beta}_1 + \hat{r}_{\hat{\beta}_0,\hat{\beta}_1}\left[\frac{\hat{S}_{\hat{\beta}_1}}{\hat{S}_{\hat{\beta}_0}}\right]\left[\beta_{0,j} - \hat{\beta}_0\right]\end{aligned}, \tag{10}$$

which is obtained by replacing Equations 8 and 9 in Equation 7. For each trial (indexed by j), a β_0 value is selected from the normal probability distribution defined by its estimate and standard error, and then the mean β_1 value is computed by using Equation 10.

The variance of the estimate is the $\hat{\beta}_0$ variance due to the linear relationship with $\hat{\beta}_0$ plus a residual variance not explained by the relationship. The variance due to the relationship is directly transferred from $\hat{\beta}_0$ to $\hat{\beta}_1$ through the Monte Carlo resampling of $\hat{\beta}_0$ and its mapping onto $\hat{\beta}_1$ by using Equation 10. The residual variance must be added in each trial with

$$\hat{S}^2_{\hat{\beta}_1,residual} = \hat{S}^2_{\hat{\beta}_1}\left(1 - \hat{r}^2_{\hat{\beta}_0,\hat{\beta}_1}\right), \tag{11}$$

where $\hat{r}^2_{\hat{\beta}_0,\hat{\beta}_1}$ = the proportion of variance due to the linear relationship.

Note in Equation 10 that when r=0, the mean of the $\hat{\beta}_{1j}$ for all j would just be the $\hat{\beta}_1$ estimate, which means that β_0 and β_1 values are independently selected in each trial; note also in Equation 11 that the resampling variance of the estimate would be its total variance. On the other hand, when $r=|1|$, Equation 11 shows that the resampling variance of β_1 would be totally due to the mapping of β_{0j} onto β_{1j}, which is expected when the linear relationship between two variables is deterministic. In this case, the algorithm presented here would only perform one Monte Carlo simulation, that on β_0. Therefore, the algorithm is flexible enough to cover the whole range of correlation between both parameter estimates.

A confidence interval for $l_{P\%}$ may be obtained by the percentile method (Casella and Berger, 1990; Efron and Tibshirani, 1993), for which two computational alternatives are available. If the resampling through the bivariate normal distribution is unbounded, then the 100(1–α)% confidence interval is obtained by ordering the $l_{P\%,j}$ from smallest to largest, and taking as bounds the values at positions $N_{MC}(\alpha/2)$ and $N_{MC}(1-(\alpha/2))$, where N_{MC} is number of Monte Carlo trials. If the resampling through the bivariate normal distribution is bounded, with bounds $\alpha/2$ and $1-\alpha/2$, then the 100(1–α)% confidence interval limits are obtained as the first and last quantiles when ordering the $l_{P\%,j}$ from smallest to largest.

Monte Carlo simulation

To test the performance of the three procedures in estimating $l_{P\%}$ for different sample sizes, we carried out a simulation analysis of a model population with known size-at-age structure, maturity-at-size, and mortality parameters (Table 2). We explored only the behavior of the methods for median (50%) size at maturity ($l_{50\%}$). Performance was evaluated by using four criteria. First, as the proportion of times that confidence intervals did contain the true (and known) parameter ($l_{50\%}$), which we call success:

$$success = 1 - failure = 1 - \frac{number\{(true - lower)(upper - true) < 0\}}{number\ of\ iterations}, \quad (12)$$

Our second criterion was bias, evaluated as the average, over trials, of the sufficient statistic:

Table 2

Parameter estimates used in the model to generate simulated data. Growth and maturity functions given by Roa (1993a) for female squat lobsters (*Pleuroncodes monodon*). Natural mortality rate (M) given by Roa (1993b) for the same species.

Parameter	Value
Size-at-age	
σ^2	4
Growth	
L	44.55
k (/yr)	0.179
t_0 (/yr)	–0.51
Maturity	
α	1
β_0	13.648
β_1	–0.502
$l_{50\%}$ (mm)	27.2
Natural mortality	
M (/yr)	0.6

$$bias = \frac{resampled\ median}{true}, \quad (13)$$

which is 1 for an unbiased estimator. The third criterion was the length of confidence intervals:

$$length = upper - lower, \quad (14)$$

and the fourth and final criterion was the shape of the interval (Efron and Tibshirani, 1993):

$$shape = \frac{upper - median}{median - lower}, \quad (15)$$

which measures asymmetry around the median. In all four measures of performance, "upper" and "lower" refer to the bounds of the confidence interval, "median" is the median $l_{P\%}$, and "true" refers to the true value. The deterministic and stochastic features of our simulation were chosen for a population with features like those previously reported for the squat lobster (*Pleuroncodes monodon*) from the continental shelf off central Chile (Roa, 1993a, 1993b).

To accomplish this task, we implemented the following three-step algorithm, which we called MATSIMVL: step 1, generation of N_{iter}=5000 random samples of maturity-at-size data of sample size N_{sample}= 500, 1000, 3000, 5000, and 10,000 individuals (Eqs. 16–19); step 2, estimation of the parameter vector and covariance matrix for each one of these samples (Eqs. 1 and 2); and step 3, running each of the three methods to obtain the 2.5%, 50%, and 97.5%

percentiles of $l_{50\%}$ (Eqs. 3–11) In bootstrap, for each sample size and each of the 5000 trials, we obtained N_{boot}=5000 bootstrap samples. With the Monte Carlo method, we resampled parameter estimate values from unbounded normal distributions with N_{MC}= 5000. For completeness, $N_{Fieller}$=1.

In step 1, the deterministic size structure of the population was conceived as a mixture of normal probability distributions, each normal distribution corresponding to an age class. The proportion of individuals at each size interval was characterized by the following expression

$$p_{n_l} = \frac{\sum_{t=0}^{9} \frac{p_{n_t}}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{1-\mu_t}{\sigma}\right)^2\right]}{\sum_{l=0}^{40}\sum_{t=0}^{9} \frac{p_{n_t}}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{1}{2}\left(\frac{l-\mu_t}{\sigma}\right)^2\right]}, \quad (16)$$

where the sum is over 10 age classes (0 to 9) and 41 size classes (0 to 40), and where μ_t is determined by a growth equation

$$\mu_t = \mu_\infty \left(1 - e^{-k(t-t_0)}\right) \quad (17)$$

with known parameters (Table 2). Variance of size-at-age (σ^2) is known and constant through age (Table 2), and the proportion of individuals at age (P_{nt}) is given by a simple exponential mortality model

$$P_{n_t} = \frac{e^{-Mt}}{\sum_{t=0}^{9} e^{-Mt}}, \quad (18)$$

where the mortality rate (M) is known and constant through age (Table 2).

Random variability came from two sources. First, samples of the specified sizes were drawn, for each trial, from a uniform probability distribution and compared with the cumulative distribution of Equation 16, accumulating the scores in the respective size intervals. This computation yielded a sample of relative size frequencies p_{nl}. Next, we introduced the second source of uncertainty by assessing the maturity status (mature or immature) of individuals belonging to each size class. This random assignment of maturity status came from resampling the binomial probability distribution

$$P(n = n_{rand}) = \binom{n_{l,rand}}{n_{rand}} P(l)^{n_{rand}} \left(1 - P(l)^{(n_{l,rand} - n_{rand})}\right), \quad (19)$$

where $P(l)$ was computed from the logistic model (Eq. 1) with known maturity parameters (Table 2) and n_{rand} is the random number of mature individuals out of $n_{l,rand}=N_{sample} \times p_{nl}$ individuals in the size interval l. In this way, step 1 was completed by randomly assigning two properties to each data individual: a size (continuous variable) and a maturity status (dichotomous variable). With these data, step 2 was completed by using a nonlinear parameterization of the logistic model (Eqs. 1 and 2) for obtaining estimates of β_0 and β_1, and their covariance matrix, by means of the SIMPLEX algorithm (Press et al., 1992). Having this information in hand, step 3 was completed by obtaining 2.5%, 50%, and 97.5% percentiles by each of the three methods. We programmed the MATSIMVL algorithm using Microsoft FORTRAN for PowerStation 4.0 (Microsoft Corp., 1995).

In the case of the Monte Carlo algorithm, we also investigated the effect of the natural mortality parameter, by varying its level in simulation at M=0.2, M=0.4, M=0.6, and M=0.8, for sample sizes of N_{sample}=1000 and 5000 individuals. N_{iter} and N_{MC} were both kept at 5000.

Finally, we introduce real data to show two applications of the Monte Carlo method developed here. First, we estimate $l_{P\%}$ (N_{MC}=5000) for a single population of the galatheid decapod *Pleuroncodes monodon*. In this application, we estimate size confidence intervals for percentages of maturity from 10% to 90% at steps of 10%. In this way a confidence interval for the whole maturity curve is outlined. Second, we compare samples of female anchovy *Engraulis ringens* from two localities 3° of latitude apart (N_{MC}=5000) to test the null hypothesis of equal $l_{50\%}$ between them.

Results

The simulation analysis with MATSIMVL yielded size-at-age and maturity-at-size data with the appropriate behavior as N_{sample} increased: size-frequency distributions became smoother and maturity data more closely followed a logistic curve, as shown by one example output of MATSIMVL data-simulating routines (Fig. 1).

A summary of the simulation results is presented in Fig. 2. It shows that, under the simulation conditions, the Monte Carlo method outperformed the bootstrap and the Fieller methods in proportion of success at all sample sizes and that it remained very close to the nominal 95%; the bootstrap method succeeded 94% or less at all sample sizes, whereas the Fieller method was unstable between sample sizes of 500 to 5000, with a minimum of 93% success at 3000 (Fig. 2A). All three methods showed negligible

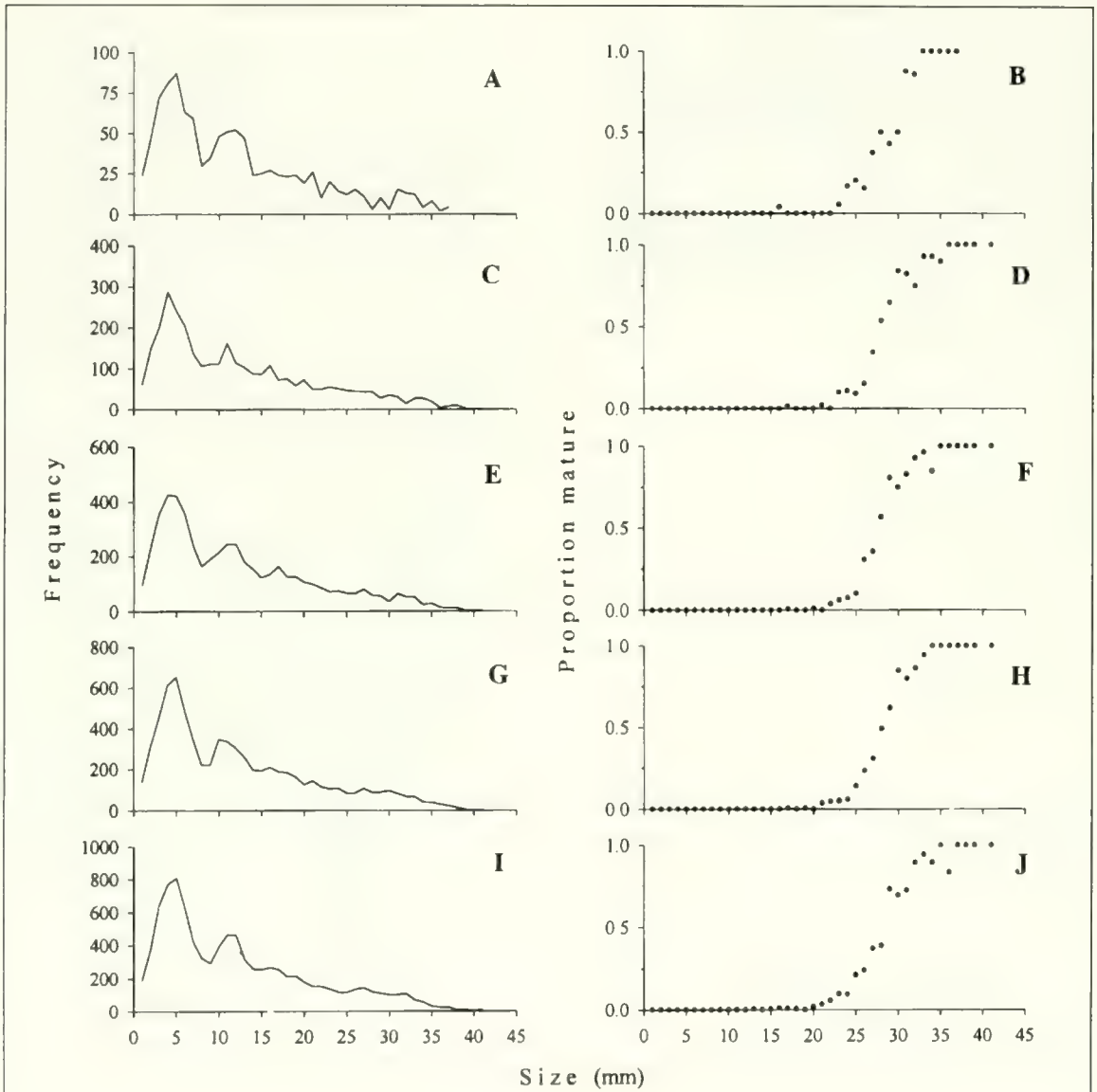

Figure 1

Example output of simulated data on size frequency and maturity-at-size generated by one trial of the MATSIMVL algorithm, for sample sizes of 500 (**A** and **B**), 1000 (**C** and **D**), 3000 (**E** and **F**), 5000 (**G** and **H**), and 10,000 (**I** and **J**) individuals.

bias at low sample sizes and converged neatly to null bias at large sample sizes (Fig. 2C). Likewise, the three methods behaved exactly the same in length of confidence interval, decaying exponentially as sample size increased (Fig. 2C). Finally, both resampling methods yielded asymmetrical (right-tailed) confidence intervals, converging to the same shape value (ca. 1.1) as sample size increased (by definition, Fieller's method yields a symmetrical confidence interval with shape=1).

Percentage success and bias of the Monte Carlo method under our model for data generation were fairly insensitive to changes in natural mortality M (Fig. 3) for sample sizes of 1000 and 5000 individuals. Percentage success remained close to the nominal 95% and bias was negligible. The length of the confidence interval and asymmetry, however, increased with increasing mortality, showing that estimation variance was directly proportional to natural mortality rate.

Results of the Monte Carlo algorithm with real data on female squat lobster are shown in Figure 4. The Monte Carlo confidence interval for $l_{50\%}$ was fairly narrow (25.86 to 28.51 mm carapace length),

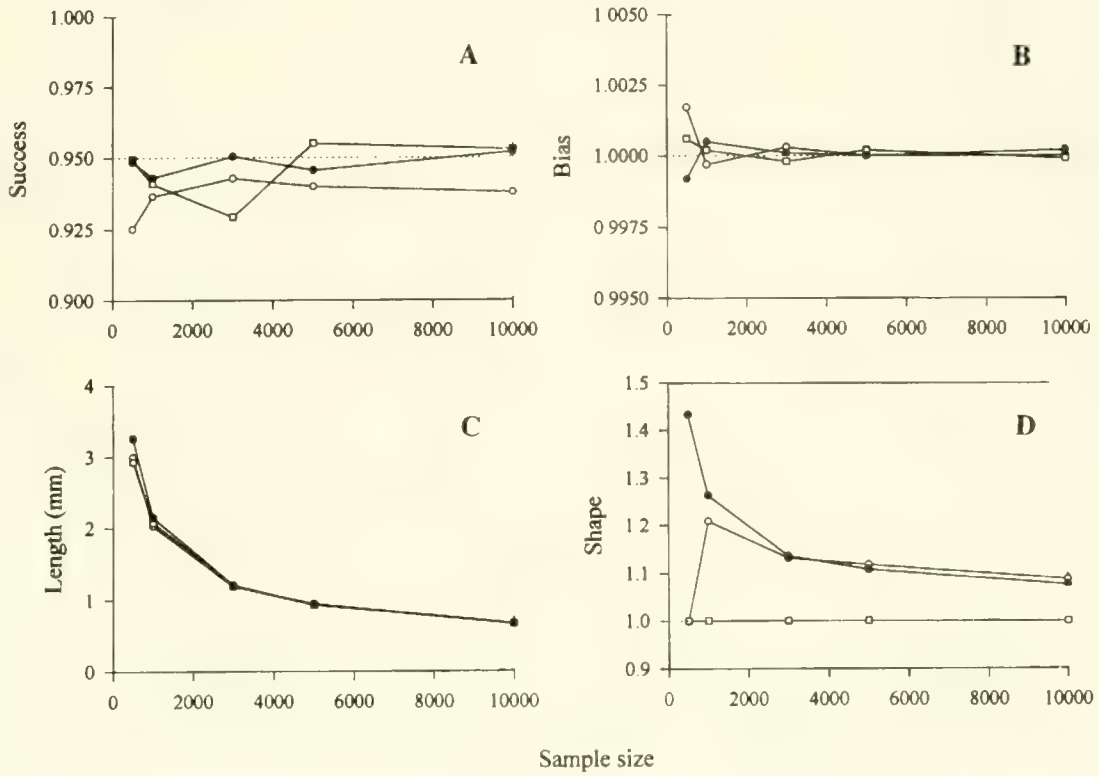

Figure 2

Summary of results from the application of the three methods to simulated data. Open squares = Fieller's analytical method; open circles: bootstrap; closed circles = Monte Carlo.

reflecting the effect of large sample size (N_{sample}= 4458). The Monte Carlo median $l_{50\%}$ (27.19 mm carapace length) coincided with the MLE of $l_{50\%}$=–MLE (β_0)(MLE(β_1). The amplitude of the confidence interval for $l_{P\%}$ showed an increasing trend towards extreme values of P (Fig. 4), a reflection of the algebraic structure of Equation 3. Results of the second application with two samples of female anchovies are shown on Figure 5. Although different in their lengths, probably due to different sample sizes, confidence intervals from the two samples overlapped and have the same upper limit. This result provides support to the hypothesis of equal maturity schedules between female anchovies from the two localities.

Discussion

The logistic model is universally used as a mathematical description of the relation between body size and sexual maturity. To model residuals, however, two different approaches emerge: to consider them normally or binomially distributed, and closely related to this, to use the data as proportions or as counts. In the first (as far as we know) formal treatment of the problem, Leslie et al. (1945) used the data as proportions, transformed to probit scores, and assumed the normal distribution. Current researchers have not employed probit transformations (but see Lovrich and Vinuesa, 1993) but have continued using data as proportions and the normal distribution for residuals (Table 1). In this work however, and following the arguments by Welch and Foucher (1988), we emphasize the need to estimate the maturity model using the data as counts and therefore to consider residuals as binomially distributed. Under this approach, the standard procedure for fitting the maturity model is logistic regression (Hosmer and Lemeshow, 1989).

When the model has been fitted, the problem of setting a confidence interval for the level of the predictor variable (size) that gives rise to a fixed proportion of maturity is not trivial. We have explored here three approaches: one analytical method based

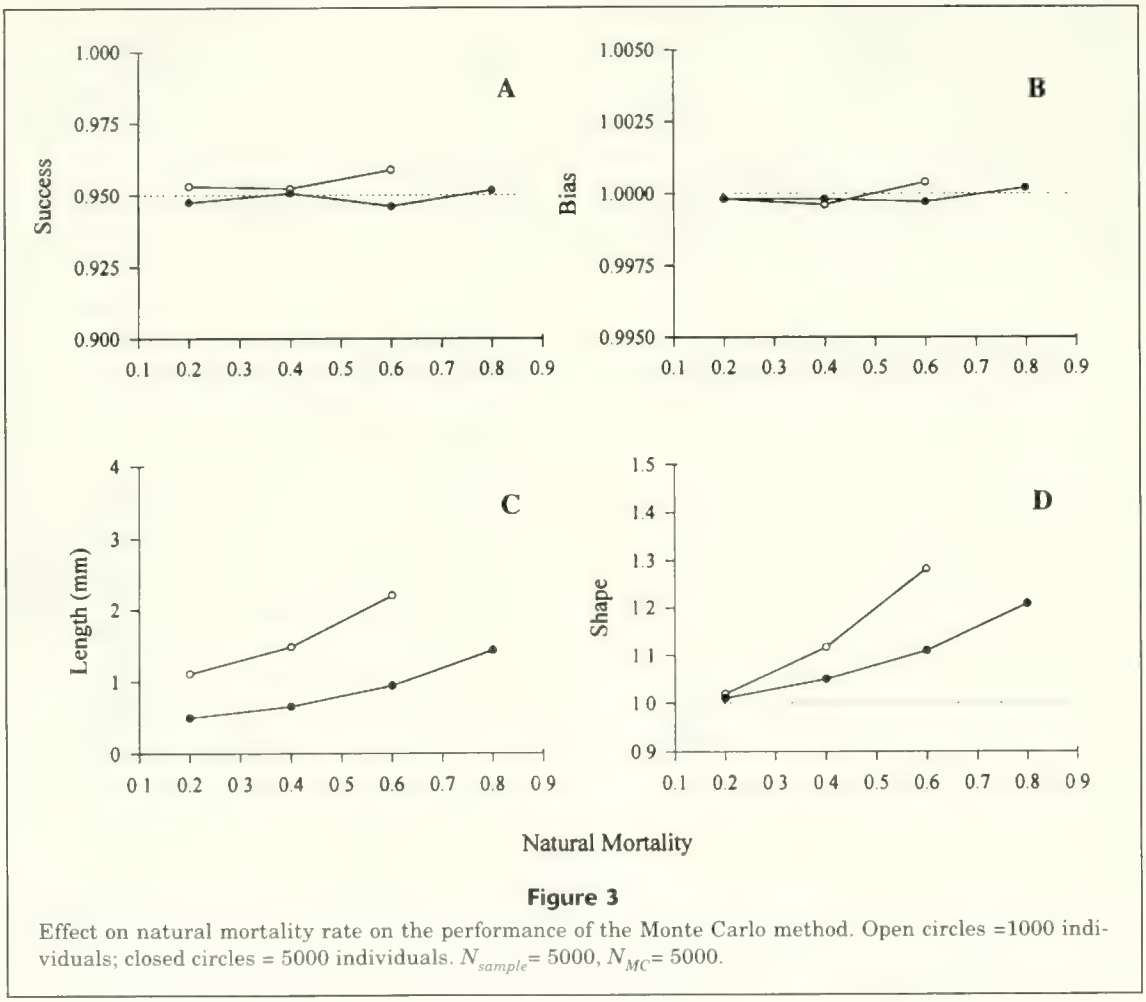

Figure 3

Effect on natural mortality rate on the performance of the Monte Carlo method. Open circles =1000 individuals; closed circles = 5000 individuals. N_{sample}= 5000, N_{MC}= 5000.

on Fieller's (1944) theorem and the logit link function, and two computationally-intensive methods based on nonparametric bootstrap of the observational pair (l_i, h_i) and Monte Carlo resampling of parameter estimates from the logistic model. Although this is not an exhaustive set of methods (for example, we did not explore likelihood profiles), they represent a set of conceptually different alternatives to be tested against the model we used to generate simulated data. In particular, both resampling methods are especially useful to obtain the distribution of a function of estimated parameters, such as in Equation 3, mainly because of their mathematical simplicity, which comes at the expense of extensive computation. Our results indicate that the three methods to estimate size at P% maturity perform almost equally well in terms of bias, length, and shape of the confidence interval, but that Monte Carlo performed better in containing the true parameter within its confidence bounds with the nominal 95% rate. This greater accuracy is accompanied by N_{boot}–1 times less computation than bootstrap.

Bootstrap single assumption was that all observations from any given sample have the same probability to appear in a new sample. In contrast, the Monte Carlo method assumed a bivariate normal distribution of parameter estimates of the maturity model. Having simpler assumptions, it is unclear why the bootstrap method failed more than the nominal 5% of the times at low sample sizes. One reasonable explanation is that for every sample, there would be N_{boot} bootstrap samples, and therefore N_{boot} numerical solutions to the normal equations under the binomial likelihood model. We used here 5000 bootstrap samples and the SIMPLEX algorithm (Press et al., 1992). Small errors in the numerical algorithm coupled with a minimum bias, may add to the nominal 5%, accounting for the 1% to 2% increase in failure rate. In contrast, the Monte Carlo algorithm requires a single numerical solution so that it does not accumulate numerical errors. On the other hand, Fieller's analytical method requires a more complicated set of assumptions than the Monte Carlo approach. Fieller's method requires normality of a lin-

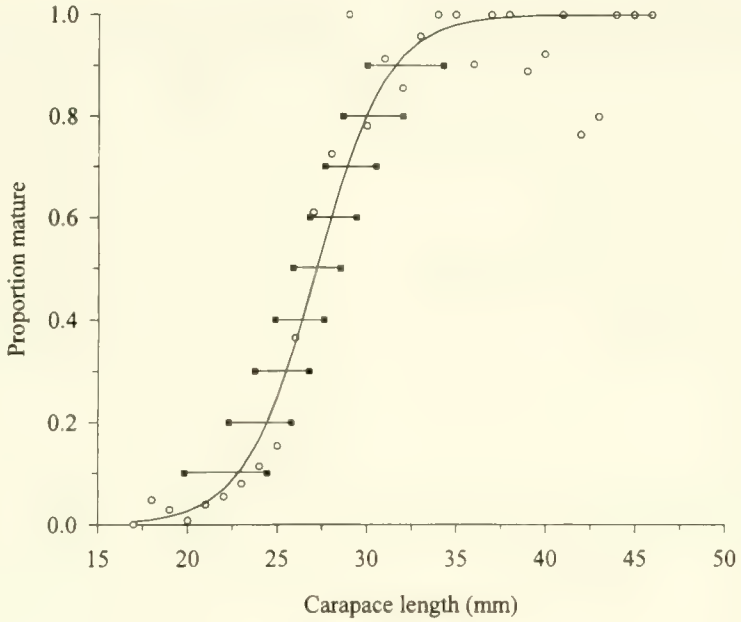

Figure 4

Monte Carlo confidence intervals for P% maturity for female squat lobsters, *Pleuroncodes monodon* (N_{sample}=4458, N_{MC}=5000). Open circles = raw data; continuous line = fitted model; closed squares = Monte Carlo confidence bounds for length at P% maturity (P=0.0–1.0 in steps of 0.1).

ear combination of parameter estimates and therefore assumes a symmetric interval estimate. Both bootstrap and Monte Carlo results indicate that the interval estimate can be quite asymmetric. This may account for the better performance of Monte Carlo, as compared with Fieller's, in proportion of success. These remarks, along with the facts that Monte Carlo's percentage success and bias are not affected by a natural mortality rate varying between 0.2 and 0.8, and that it is very fast on every computer platform, allows us to recommend the use of the Monte Carlo method to estimate size at P% maturity.

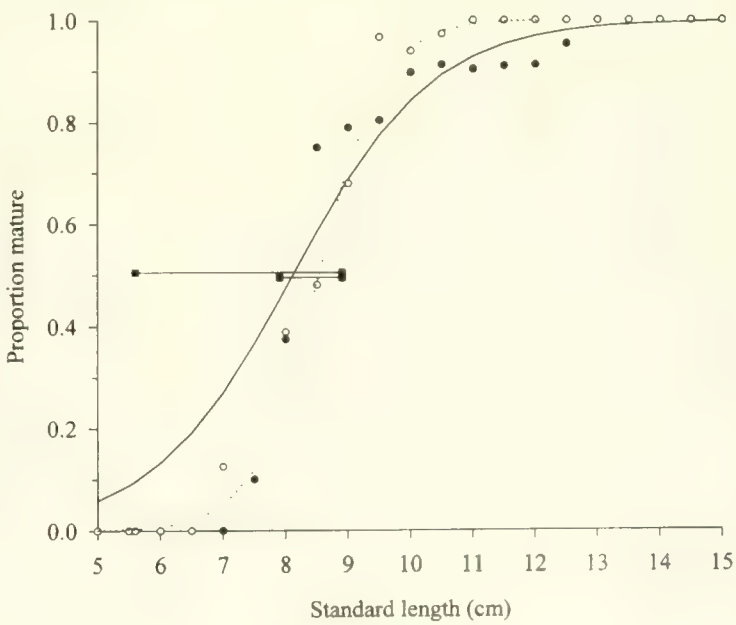

Figure 5

Monte Carlo confidence intervals for length at 50% maturity of female anchovies (*Engraulis ringens*) sampled from two localities off central Chile. Open circles and dotted line = Talcahuano (36°45'S) (N_{sample}=783, N_{MC}=5000); Closed circles and solid line = San Antonio (33°35'S) (N_{sample}=585, N_{MC}=5000); Closed squares = 95% confidence bounds for $l_{50\%}$.

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Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary*

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Abstract.—Patterns of growth and mortality were examined for postsettlement red drum, *Sciaenops ocellatus*, inhabiting seagrass meadows in the Aransas Estuary, Texas. Age and growth rates of larvae and early juveniles were estimated in 1994 and 1995 by using daily increments in otoliths. Otolith-derived estimates of age indicated that individuals spend approximately 20 d in the pelagic environment before entering demersal habitats (i.e. before settlement). Instantaneous growth coefficients (g) of red drum ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995. Site-specific differences in growth were also examined and a significant site effect was detected in 1994; however, no site effect was observed in 1995. Interannual and cohort-specific (10-d cohorts) mortality rates were estimated from declines in $\log_e$ abundance (abundance-at-age plots), and results indicated that mortality during the early postsettlement period was substantial. Instantaneous mortality coefficients (Z) were similar between years (0.134 [12.5%/d] in 1994; 0.139 [13.0%/d] in 1995), and no significant interannual effect was observed. Conversely, cohort-specific mortality rates ranged widely (0.106–0.265 [10.1–23.3%/d]) and losses were lowest for midseason cohorts. Recruitment potential ($G:Z$ ratio) was highest for midseason cohorts (1.30–1.56) and lowest for early and late-season cohorts (<1). Although $G:Z$ ratios varied over spatial and temporal scales, ratios were >1 in 1994 and 1995, suggesting that both year classes experienced favorable nursery conditions.

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Survival during the larval and juvenile stages of marine fishes is highly variable and plays a critical role in determining recruitment potential (Cushing, 1975; Houde, 1987). Early life survival is a function of both growth and mortality, and it is clear that these mechanisms act in concert to determine an individual's probability of survival (Houde, 1996). Individuals experiencing rapid growth will spend less time in vulnerable size ranges (reduced stage duration) and achieve a larger body size at a given age, thus enhancing their ability to detect and escape predators (Bailey and Houde, 1989; Fuiman and Magurran, 1994). Consequently, recruitment success or failure is closely linked to variation in growth and mortality during the early life stage.

Much of our current understanding of early life growth and mortality is based on information derived from the examination of otolith microstructures. The daily deposition of growth increments on otoliths has been demonstrated for many marine teleosts and provides a means of estimating age, growth rate, and hatching date (see reviews by Campana and Neilson, 1985; Jones, 1986). Moreover, knowledge of a population's age structure can be combined with density data (abundance-at-age relationships) to estimate mortality rates. Thus, fundamental demographic parameters can be obtained through otolith analysis, and these data are essential for determining the causes and consequences of differential survival.

Red drum (*Sciaenops ocellatus*) inhabit subtropical and temperate waters in the Western Atlantic and support important commercial and recreational fisheries throughout the coastal waters of the Gulf of Mexico (Swingle, 1990; NOAA, 1991). Red drum spawn in the early fall in offshore waters and areas near tidal inlets, and tidal currents transport larvae through passes and into estuarine nursery habitats (Holt et al., 1989; Comyns et al., 1991). Individuals settle into sea-

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grass and marsh-edge habitats following a fairly short pelagic interval and remain in these habitats during the juvenile stage (Baltz et al., 1993; Rooker and Holt, 1997; Rooker et al., 1998b).

Although much effort has been directed toward the management of red drum stocks, research on growth and survival during early life has received limited attention. As a result, the aim of this study was to examine spatial and temporal patterns of growth and mortality during the postsettlement period. Specific objectives of this research were to estimate annual variation in growth and mortality, to estimate cohort- and site-specific mortality rates, and to determine the recruitment potential of different cohorts.

Materials and methods

Field collections

Red drum were collected from two shoal grass (*Halodule wrightii*) meadows in the Aransas Estuary, Texas (Aransas Bay 1 and 2 [AB1, AB2]; Fig. 1), during the annual settlement period (August–December). Collections were taken over a two-year period (1994–95) with an epibenthic sled measuring 0.75 (w) × 0.5 (h) m, equipped with a 505-µm mesh conical plankton net. Triplicate 20-m sled tows were taken every week at each site in 1994. A more comprehensive sampling strategy was employed in 1995 in order to evaluate cohort-specific variation in natural mortality. Ten 20-m sled tows were taken every 3–4 d at each site during the entire 1995 settlement season. Red drum larvae and juveniles were preserved in 70% ethanol immediately after capture. Environmental data collected at each site included depth, salinity, and water temperature.

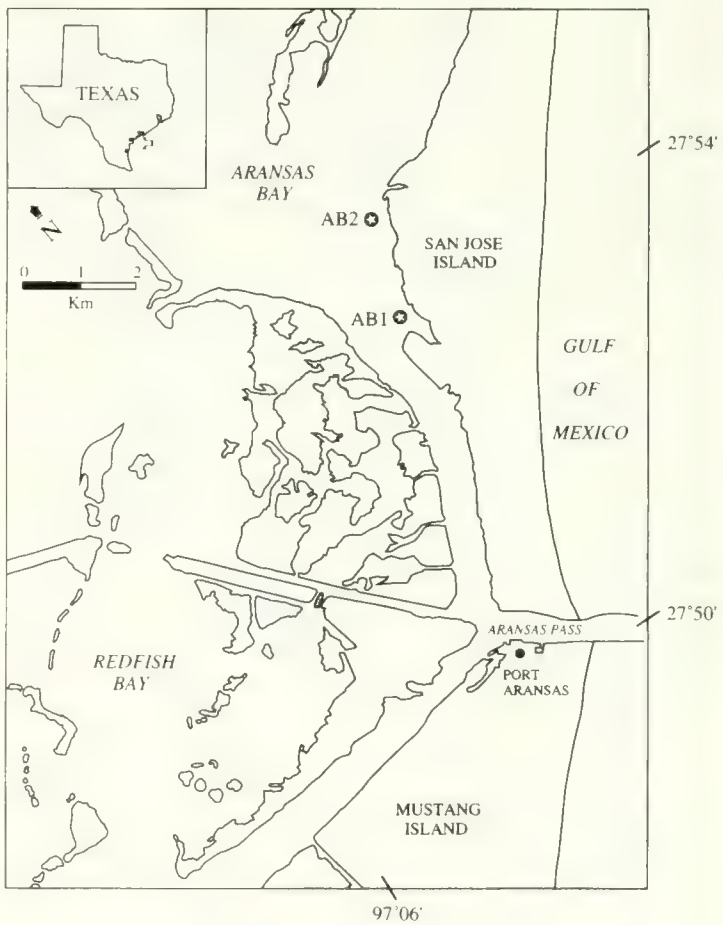

Figure 1

Location of shoal grass (*Halodule wrightii*) sampling stations (AB1 and AB2) in the Aransas Estuary, Texas.

Laboratory procedures

Removal and processing of otoliths (lapilli) followed the procedures described by Rooker and Holt (1997). Otolith radius, increment count, and increment widths were measured on a straight line from the core to the posterior edge using an image analysis system (Optimas, Bioscan). Because otolith growth is allometric (Campana and Neilson, 1985), all measurements were taken in the same field. Daily deposition of increments was validated in our laboratory by chemically marking the otoliths of known-age red drum with alizarin complexone (S.A. Holt, unpubl. data).

Age was determined by enumerating growth increments from the core to the margin of the otolith. Inner increments (proximal to the core) on lapilli were often difficult to enumerate. Thus, in order to accurately determine the age of wild red drum, a relationship between age and otolith radius from laboratory-reared red drum was developed and used to predict the number of growth increments at various distances from the core (Rooker and Holt, 1997). Age was determined by adding the predicted age from the unreadable section (correction factor from age-radius relationship) to the increment count (number of increments from first identifiable increment to edge of the lapillus). Correction factors generally accounted for less than 25% of the actual age estimate, and the relative size of the correction did not differ between years. Both the left and right lapilli were examined and estimates of age and growth were derived by averaging readings from both otoliths. On average, age differences between otoliths were small (CV=3.6%: range 0–14%). For some individuals

(18%), only one of the lapilli was available owing to loss, breakage, or staining.

Growth rates were determined by using otolith-derived estimates of age (size-at-age plots) in 1994 (n=249) and 1995 (n=140). Daily instantaneous growth coefficients were calculated from an exponential model described as

$$L_t = L_0 e^{gt},$$

where L_t = length (mm SL) at time t;
L_0 = the estimated length at hatching;
g = the instantaneous growth coefficient (/d); and
t = the otolith-derived age (days after hatching).

Ages of red drum not assessed with otolith-based techniques (1994 [n=1,057], 1995 [n=8004]) were estimated by using age-length relationships.

Weight-specific instantaneous growth coefficients (G) were calculated by using the equation

$$W_t = W_0 e^{Gt},$$

where W_t = the wet weight (mg) at time t;
W_0 = the estimated weight at hatching;
G = the weight-specific instantaneous growth coefficient (/d); and
t = the otolith-derived age.

Red drum lengths (mm) were converted to wet weight (mg) by using a polynomial equation (third order) based on measurements from laboratory-reared red drum (range: 6–30 mm): $W = -7.745 + 2.122L - 0.205L^2 + 0.024L^3$ (n=200, r^2=0.97), where W and L represent wet weight and standard length, respectively.

Mortality rates were estimated from regressions of the decline in $\log_e$-transformed abundance on age. Although interannual variation in mortality was examined by pooling individuals from each year (all cohorts combined), cohort-specific rates were based on regression plots of $\log_e$-transformed abundance of individuals from 10-d cohorts determined from hatching-date analysis. Hatch dates of individual red drum were determined by subtracting the otolith-derived age from the date of collection. Hatching dates were then used to separate individuals into specific cohorts, defined as individuals hatched within a 10-d period. Each cohort was designated by a letter (A to F): 1–10 Sep (A); 11–20 Sep (B); 21–30 Sep (C); 1–10 Oct (D); 11–20 Oct (E); and 21–30 Oct (F). Densities for the first and last cohort (A, F) were low and thus mortality regressions were not fitted to these data. Daily instantaneous mortality rates were calculated from the exponential model of decline:

$$N_t = N_0 e^{-Zt},$$

where N_t = abundance at time t;
N_0 = the estimated abundance at hatching;
Z = the instantaneous mortality coefficient (/d); and
t = the otolith-derived age.

Owing to incomplete capture (i.e. ascending limb of catch curve) of small red drum (<25 d, ≤8 mm), these individuals were not included in mortality regressions. Also, size-based gear avoidance was suspected, which placed constraints on the upper age (or size) of individuals used in regression analysis. In preliminary trials, the capture efficiency of the epibenthic sled was compared with a bag seine (seine dimensions: 7 m length × 1 m height; mesh size: 3 mm) and size-specific differences in capture efficiency (individuals/m^2 of habitat sampled) between the two gears were not detected for sciaenids <25 mm (Rooker, 1997). However, density estimates of sciaenids >25 mm were higher with the seine. This suggested that individuals >25 mm are capable of avoiding the sled and that densities calculated for these individuals would be underestimated. Consequently, only red drum between 8 and 20 mm (25–40 d) were used to estimate mortality rates.

Our assessment of early life mortality was based on two assumptions: 1) individuals entering seagrass sites remained in these habitats (i.e. settle and stay) during the time period when mortality rates were estimated, and 2) immigration and settlement (i.e. late settlers) to the designated study sites from other locations or habitats, or both, was negligible. Although postsettlement movement (emigration or immigration, or both) can be important for certain species and failure to account for such movements can severely bias mortality estimates (Frederick, 1997), our assumptions are reasonable because red drum appear to settle and stay in seagrass meadows at least through the early juvenile stage (Rooker et al., 1998b). Furthermore, no salient increases or decreases in density were observed in length-frequency profiles which would be expected in the presence of postsettlement emigration or immigration activity.

Since total mortality (Z) is the sum of both natural (M) and fishing mortality (F), it is important to account for the fishing mortality (F) caused by our sampling (Ricker, 1975). Most studies evaluating early life mortality do not estimate F (=sampling mortality) and assume F to be inconsequential. In this study, seagrass meadows of limited size (ca. 25,000 m^2) were sampled repeatedly and, as a result, the effect of F was considered potentially significant. Therefore, mortality regressions were run on abundance data

adjusted to compensate for sampling losses (F). Abundance at each sampling time was adjusted by subtracting the number of individuals collected (removed from population) with the epibenthic sled from the overall abundance at the site (site abundance = area of site/area sampled × number of red drum collected). Regressions of $\log_e$-adjusted abundance on age were then run and mortality coefficients derived in this manner were basically estimates of M since the effect of F was removed. Consequently, F was determined by subtracting adjusted mortality rate (M) from Z. Because F values were relatively small, 2.3 to 6.9% of Z, only estimates of Z are presented.

The relative recruitment potential of individual cohorts was assessed by examining the ratio of weight-specific growth (G) to mortality (Z). The ratio is commonly used as an index of stage-specific survival because it incorporates both growth and mortality (Werner and Gilliam, 1984; Houde, 1996). Because cohorts with $G:Z$ ratios >1 gain biomass, the probability of survival (recruitment potential) for these individuals is assumed to be high.

Data analysis

Analysis of covariance (ANCOVA) was used to test for intra- and interannual differences in growth and mortality (covariate: age). Prior to each ANCOVA test, a preliminary model (interaction regression) was tested to determine if the slopes of the regression lines differed (homogeneity of slopes assumption; Sokal and Rohlf, 1981). The main significance test of the ANCOVA (homogeneity of y-intercepts) was performed when the parallelism of slopes assumption was met. Since differences in abundance affect the elevation of regression plots used to estimate mortality, spatial and temporal trends in mortality were evaluated by comparing slopes (y-intercept test not performed). Analysis of variance (ANOVA) was used to examine variability in density. Estimates of density were $\log_e$-transformed to minimize heteroscedasticity.

Results

Environmental conditions

Water temperature and salinity were recorded daily from August to December in 1994 and 1995. Temporal variation in both parameters was pronounced and trends were similar between years (Fig. 2). Temperature during the primary settlement period was variable (September–October) and ranged from 23.3° to 30.2°C in 1994 and from 22.7° to 31.6°C in 1995, respectively. Mean temperature during this period was similar between years 1995 (27.5°C) and 1994 (27.2°C). Salinity ranged from 25.3‰ to 37.0‰ and from 25.3‰ to 30.8‰ in 1994 and 1995, respectively. Similar to temperature, mean salinity was relatively similar between years: 30.0‰ (1994) and 28.6‰ (1995). Peak values for both parameters occurred during the initial spawning period and declined for later spawning and settlement dates. Cohorts arriving early in the season experienced high temperature and salinity, whereas late-season cohorts were exposed to lower temperature and salinity (Fig. 2). No conspicuous differences in temperature or salinity were observed between sampling sites (AB1, AB2).

Catch characteristics

Overall, 1306 and 8144 red drum larvae and early juveniles (3–40 mm) were collected from the two sampling sites in the Aransas Estuary in 1994 and 1995. In both years, settlers were first detected in early September and peak densities of recently settled red drum (≤10 mm) were present in early October (Fig 3). Larger postsettlers (>10 mm) were most abundant from mid-October to early November. Mean densities of recently settled red drum (<10 mm) ranged from 0.0 to 1.7/m^2 in 1994 and from 0.0 to 4.1/m^2 in 1995; densities of all postsettlement red drum (≤40 mm) ranged from 0.0 to 3.0/m^2 in 1994 and from 0.0 to 4.2/m^2 in 1995 (Fig. 3). Maximum densities (per sled tow) observed in 1994 and 1995 in the Aransas Estuary were 3.4/m^2 and 11.5/m^2, respectively. Interannual variation in postsettlement density during the two seasons (October–November) was small: 1.53/m^2 (1994), 1.63/m^2 (1995). No significant differences in density were detected between years or sites (ANOVA, P>0.05).

Although collection effort varied between years, length-frequency distributions of red drum from the Aransas Estuary were similar (Fig. 4). In both years, the smallest individuals collected were 3 mm and large recruits (>30 mm) were collected infrequently. Catch rates showed a steeply ascending left limb which peaked at approximately 8–9 mm, suggesting that recruitment to seagrass meadows was complete for these individuals. A long descending right limb characterized catches for individuals >10 mm.

Age and growth

Age-length relationships (age-length keys) were developed for each year class and described by the following equations: $Age = -17.05 + 42.25\ \mathrm{Log}SL$ (1994, n=249, r^2=0.90, CV=8.9); $Age = -11.43 + 40.11\ \mathrm{Log}SL$ (1995, n=140, r^2=0.90, CV=7.5). Predicted ages of red drum (3–30 mm) ranged from 6 to 45 d in 1994 and from 10

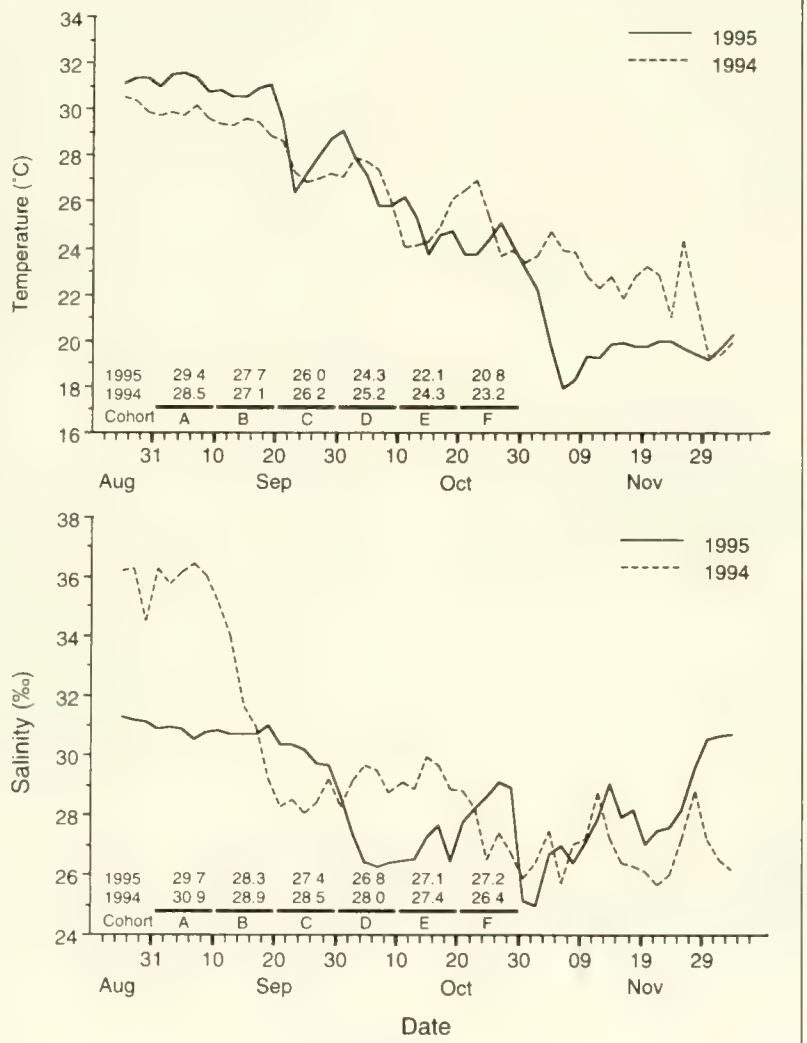

Figure 2

Water temperature and salinity records for the Aransas Estuary in 1994 and 1995. Mean temperature and salinity (30-d average) experienced by red drum cohorts (A–F) are given.

to 48 d in 1995. Individuals from the most abundant size class (8–10 mm) were approximately 20–28 d. Age data were used to determine hatch dates and these data were used to partition individuals into 10-d cohorts.

Instantaneous growth coefficients (g) ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995 (Fig. 5) and differed significantly between years (ANCOVA, *y*-intercepts, $P<0.001$). Instantaneous growth coefficients were also estimated on a site-specific basis within the Aransas Estuary (Table 1). In 1994, growth rates at AB1 were significantly higher than AB2 (ANCOVA, *y*-intercepts, $P=0.015$); however, no site effect was observed in 1995 (ANCOVA, *y*-intercepts, $P=0.440$). The weight-specific growth coefficients (G) ranged from 0.159 to 0.162 (14.7–15.0%/d) and from 0.163 to 0.165 (15.0–15.2%/d) in 1994 and 1995, respectively (Table 1).

Mortality

Instantaneous mortality coefficients (Z) ranged from 0.134 (12.5%/d) in 1994 to 0.139 (13.0%/d) in 1995 and no significant interannual effect was observed (ANCOVA, slopes, $P=0.737$) (Fig. 6). Stage-specific mortality rates (cumulative mortality during the early postsettlement period: 12-d period, ca. 10–20 mm) ranged from 1.668 (81.1%) to 1.608 (79.9%) in 1994 and 1995, respectively. Spatial variation in mortality was also examined within each year by estimating mortality rates at the two sites within

the Aransas Estuary. Site-specific mortality rates in 1994 ranged from 0.129 to 0.141 and no significant difference was detected between sites (ANCOVA, slopes, P=0.741); however, in 1995 mortality rates were significantly lower in AB1 (0.129) than in AB2 (0.193) (ANCOVA, slopes, P=<0.001).

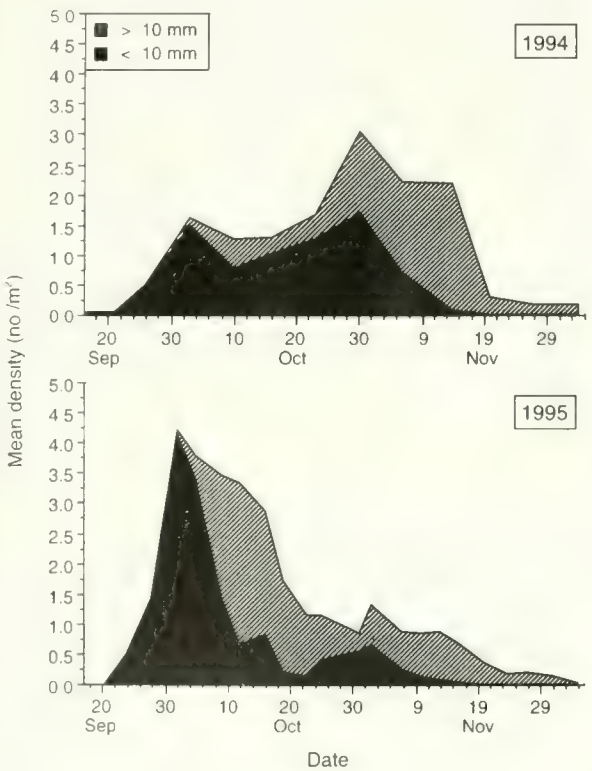

Figure 3

Mean density (sites pooled) per sampling trip of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Two size classes of postsettlement red drum (≤10 mm SL, >10 mm SL) are shown.

Table 1

Growth and mortality coefficients of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. The *G:Z* recruitment index is also shown.

Year	Site	g	G	Z	$G:Z$
1994	AB1	0.051	0.159	0.141	1.128
	AB2	0.048	0.161	0.129	1.248
	All sites	0.049	0.162	0.134	1.209
1995	AB1	0.052	0.165	0.129	1.279
	AB2	0.049	0.163	0.193	0.845
	All sites	0.051	0.165	0.139	1.187

Cohort-specific mortality rates were estimated for the 1995 year class (Fig. 7). Instantaneous mortality coefficients for 10-d cohorts ranged from 0.106 (10.1%/d) to 0.265 (23.3%/d) and a significant temporal trend was detected (ANCOVA, slopes, P=0.004). Mortality rates were lowest for midseason cohorts (C, D) and highest for early and late cohorts (B, E), and individuals from the last cohort (E) experienced the greatest mortality. Stage-specific mortality rates (10–20 mm, 12 d) ranged from 1.272 to 1.524 (71.9–78.2%) for midseason cohorts and 2.316 and 3.180 (90.1–95.8%) for early and late-season cohorts.

G:Z Index

Recruitment potential of different cohorts was evaluated by comparing *G:Z* ratios and temporal variation was observed (Fig. 8). The ratio of *G:Z* was highest for mid-season cohorts; 1.305 (cohort C) and 1.565 (cohort D). In contrast, *G:Z* ratios of early and late-season cohorts (B, E) were <1, suggesting that these cohorts were losing biomass. Moreover, annual estimates of *G:Z* were calculated and ratios were >1 in both 1994 and 1995. Site-specific variation was also observed and, apart from site AB2 in 1995, *G:Z* ratios were always >1 (Table 1).

Discussion

Otolith-derived estimates of age indicate that red drum enter estuarine seagrass meadows after a short pelagic interval. Peak densities were observed for individuals 8–9 mm (20–24 d), suggesting that recruitment to seagrass meadows follows a planktonic period of approximately 20 d. In support of this finding, studies examining red drum during the planktonic phase have shown that the upper size range of red drum larvae in pelagic environments is 6–8 mm (Peters and McMichael, 1987; Comyns et al., 1989; Holt et al., 1989). In addition, Peters and McMichael (1987) sampled demersal habitats in Tampa Bay, Florida, and reported that red drum were first detected at 8 mm. Consequently, red drum appear to move from pelagic to demersal habitats (i.e. settlement) at approximately 8 mm.

Once in seagrass meadows, length- and weight-specific growth of red drum increases rapidly with increasing size (exponential relationships). Length-specific growth rates of new settlers (20–40 d) in the Aransas Estuary averaged 0.58 and 0.62 mm/d in 1994 and 1995, respectively. Growth estimates in the Aransas Estuary are similar to rates reported by Peters and McMichael (1987) for red drum in Tampa Bay, Florida (0.58 mm/d). With size-at-age equations

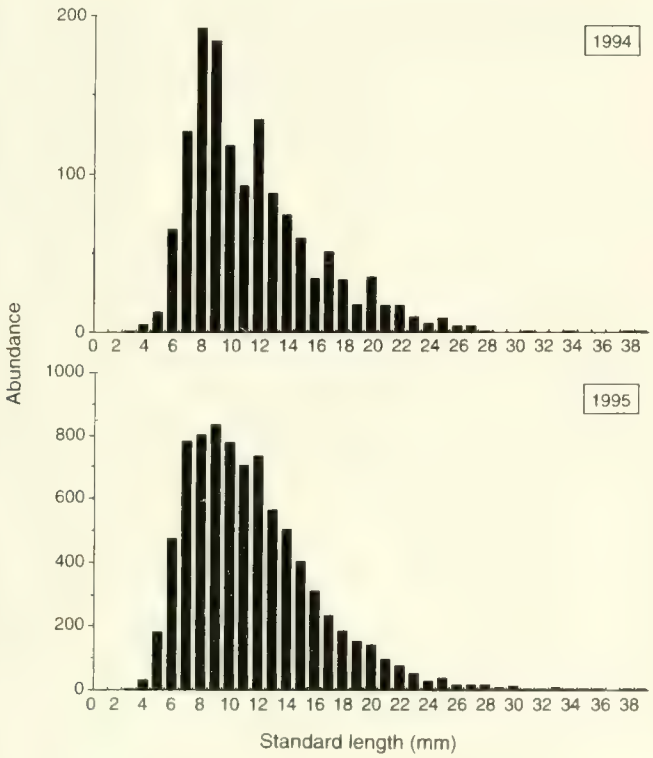

Figure 4

Length-frequency distributions of postsettlement red drum collected from the Aransas Estuary in 1994 (n=1306) and 1995 (n=8144).

Figure 5

Size-at-age relationships of postsettlement red drum collected from the Aransas Estuary in 1994 (n=249) and 1995 (n=140). Exponential equations are given.

derived for red drum, we predicted that the length of a 40-d individual ranged from 20.2 mm (1994) to 18.2 mm (1995), which was similar to the predicted length of a 40-d individual collected in Tampa Bay (20.5 mm). Although seasonal trends in growth variation were not examined in this study, Rooker and Holt (1997) observed considerable variability among cohorts of newly settled red drum (0.5–0.8 mm/d), and growth was generally highest for midseason cohorts.

Mortality rates of red drum were substantial and varied over spatial and temporal scales. Interannual estimates of mortality were similar and losses ranged from 12.5 to 13.0%/d (Z=0.13–0.14). Consequently, cumulative mortality during the settlement and early postsettlement period (12-d period) was relatively high; only about 20% of the initial settlers survived to 40 d. Although no estimates of mortality exist for red drum larvae and early juveniles, these mortality rates are comparable to values reported for other marine fishes during the early life stage. Houde (1987) reported instantaneous daily mortality coefficients for five species of marine fishes during the larval stage (first feeding to late-stage larvae) and predicted values ranging from 0.04 to 0.18 (4–16%/d). In addition, Houde and Zastrow (1993) summarized natural mortality data for teleost larvae from a variety of sources and reported that the mean instantaneous daily mortality rate of larvae in estuarine habitats was 0.266 (23%/d). Also, McGurk (1986) developed a general mortality equation for marine fish larvae (based on dry weight), and using his equation we predicted the mortality rate of individual red drum 8–10 mm (ca. 750–1500 µg dry wt) would be approximately 0.05–0.11 (4.9–10.4%/d).

Although interannual patterns of mortality were insignificant, variability within a year was relatively high and a seasonal trend was evident. Cohort-specific estimates indicated that mortality rates were lowest for red drum produced in the middle of the spawning season (10%/d), when densities within the seagrass meadows reached maximum levels. Conversely, mortality rates for early and late-season co-

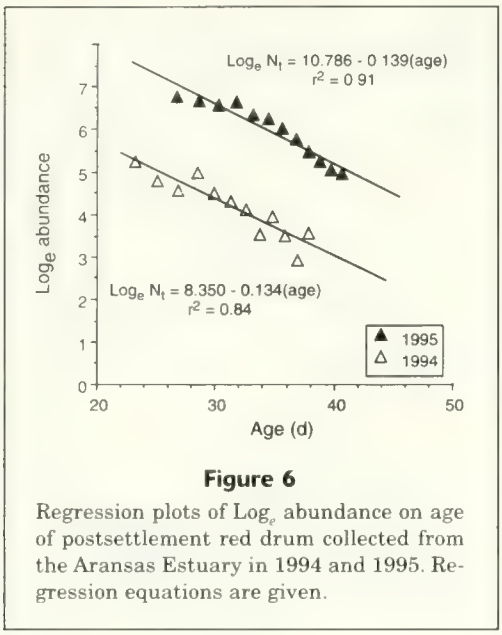

Figure 6

Regression plots of Log$_e$ abundance on age of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Regression equations are given.

horts were approximately twofold higher, approaching 25%/d for the late-season cohort. Seasonal fluctuations of this magnitude have been reported in several studies on marine fish larvae and attributed to changes in environmental conditions (e.g. temperature, prey availability) which can directly or indirectly influence mortality (Rutherford and Houde, 1995; Secor and Houde, 1995).

Temperature is often implicated as a critical factor in recruitment because it has the potential of influencing growth rates and causing episodic mortality during early life (Houde and Zastrow, 1993; Houde, 1996). Temperature has been shown to be a primary determinant of growth variation in laboratory and wild populations of red drum (Holt et al., 1981; Lee et al., 1984; Rooker et al., 1997). Moreover, Rooker and Holt (1997) determined that seasonal trends in growth variation for red drum were related to temperature. Mean temperatures experienced by successive cohorts declined throughout the season; however, growth rates were highest for mid-season cohorts (20 September–10 October) and lowest for early and late cohorts. Conversely, mortality rates were lowest for mid-season cohorts and highest for early and late cohorts. Growth and mortality data appear to be best described by curvilinear relationships (quadratic function), suggesting that there may be an optimal temperature range at which growth and survival of red drum are enhanced and that the midpoint of this range occurs at approximately 26°C.

Variability in other biotic and abiotic factors may also be responsible for observed trends in mortality. Similar to other marine fishes, growth and survival rates of red drum larvae are associated with prey availability (G.J. Holt, unpubl. data). Since spatial and temporal variation in prey density (i.e. meiofauna) are common in estuarine habitats in south Texas (Montagna and Kalke, 1992), seasonal trends in prey abundance may

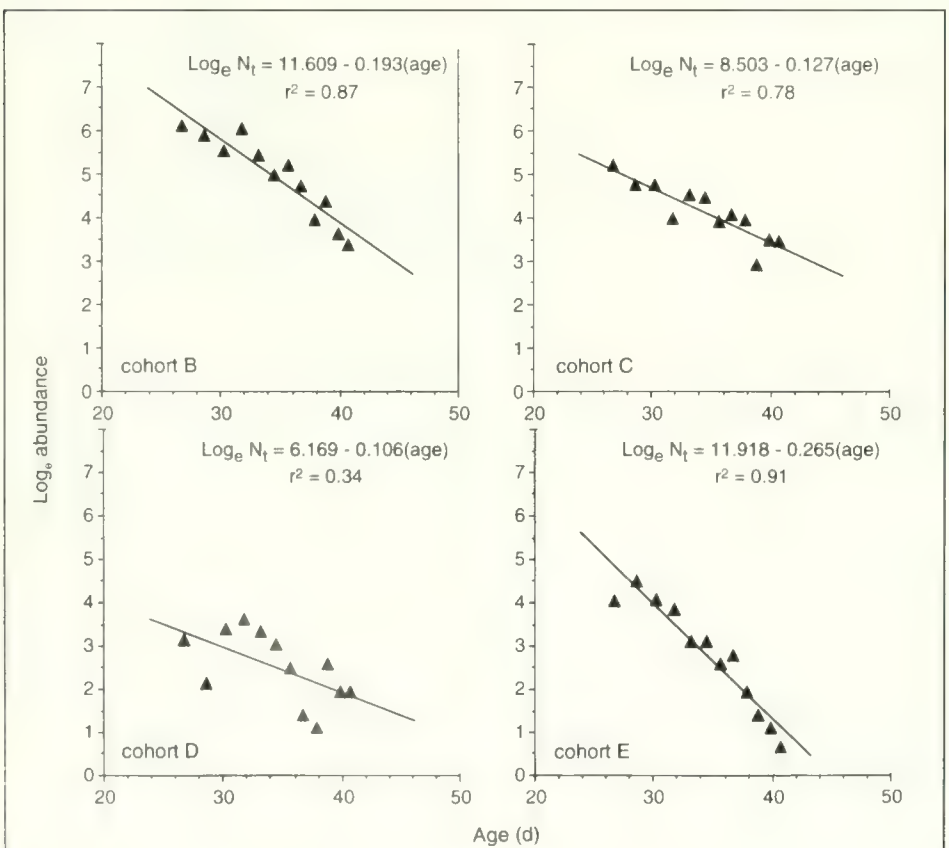

Figure 7

Regression plots of Log$_e$ abundance on age for 10-d cohorts of postsettlement red drum collected from one site (AB2) in the Aransas Estuary in 1995. Regression equations and plots are shown for cohorts B, C, D, and E.

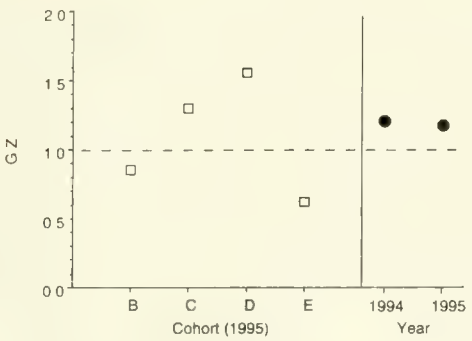

Figure 8

Recruitment potential (*G:Z* ratios) of 10-d cohorts of postsettlement red drum collected from the Aransas Estuary in 1995. Interannual estimates of *G:Z* are given.

have affected early life survival. Conversely, predator fields also vary spatially and temporally and survival may be a function of predator abundance. Postsettlement red drum are exposed to a suite of predators in the seagrass meadows and the abundance and distribution of these predators are highly variable (senior author's unpubl. data). Rooker et al. (1998a) examined predation rates on newly settled red drum in experimental mesocosms and demonstrated that predators inhabiting these seagrass meadows, are capable of consuming large numbers of red drum (Z=2–7%/[h · predator]). Consequently, fluctuations in prey and predator densities appear critical to the survival of red drum and the addition of this information to future studies should enhance our understanding of early life mortality.

Growth and mortality estimates were combined to evaluate the relative recruitment potential (*G:Z*) of red drum cohorts. According to Houde and Zastrow's (1993) review of 188 species, *G:Z* ratios for marine fish larvae are generally less than 1.0 (mean $G:Z$=0.89) and larvae inhabiting estuarine ecosystems tend to have low G:Z ratios (range: 0.34–0.82). However, recent work in Chesapeake Bay on striped bass (*Morone saxatilis*) has demonstrated that *G:Z* ratios can be >1 in estuarine ecosystems (Rutherford and Houde, 1995; Secor and Houde, 1995). Similarly, *G:Z* ratios for postsettlement red drum in the Aransas Estuary were >1 in both 1994 and 1995 (1.21 and 1.19, respectively) and, as a result, gross growth efficiency was positive and the recruitment potential of 1994 and 1995 year classes appears to have been favorable.

A high degree of correspondence in *G:Z* ratios between years was present, suggesting that conditions for growth and survival were similar in 1994 and 1995. Although the assessment of physical and biological conditions was limited (no data on prey availability or predator fields), parameters measured in this study (e.g. temperature, salinity, settlement size, and density) were relatively equal between years. In contrast, *G:Z* ratios of 10-d cohorts and the environmental conditions experienced by these individuals were highly variable within a single season. The *G:Z* ratios were highest (1.3–1.6) for midseason cohorts and settlement densities at these times were at maximum levels. Thus, it appears that physical and biological conditions in the seagrass meadows were optimal for growth or survival, or for both. The opposite trend was observed for individuals arriving early and late in the season. Because *G:Z* ratios of individuals from these cohorts were low (0.6–0.9), we postulated that nursery conditions experienced by early and late-season cohorts do not favor early life survival (low recruitment potential).

Acknowledgments

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Estimation of sablefish, *Anoplopoma fimbria*, abundance off Alaska with an age-structured population model

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Abstract.—Relative abundance of sablefish, *Anoplopoma fimbria*, in the waters off Alaska has been measured annually since 1979 with longline surveys. These extensive surveys provide precise measures of relative abundance. An age-structured model was fitted to the longline survey data to estimate absolute abundance. Estimates of recent exploitation rates for fully selected ages averaged 10%. Monte Carlo simulations of the age-structured model indicated that absolute abundance of Alaskan sablefish can be estimated reliably if age selectivity is asymptotic and not dome-shaped. Abundance estimates were reliable even when only length data and no age data were available. Dome-shaped selectivity gave biased and less precise estimates, probably owing to a parameter interaction between catchability and the shape of the selectivity function.

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Sablefish, *Anoplopoma fimbria*, is a long-lived species that inhabits the northeast Pacific Ocean and Bering Sea. This species supports a fishery in Alaskan waters, with catches ranging from about 10,000 to 35,000 metric tons (t) during the last two decades (Fig.1). The fishery mostly uses longline gear and primarily occurs on the upper continental slope, which is inhabited by adult sablefish (Fig. 2). Previously the fishery became compressed year-round during the mid-1980s to 10 days in some areas, until 1995, when management switched to individual fishing quotas and an eight-month season. The delay of the start of the season from 1 January to 1 April and later 15 May accompanied the compressed fishery season.

In Alaska, relative abundance of sablefish has been best measured by annual longline surveys since 1979. Longline surveys are preferred over trawl surveys for assessing sablefish because the longline surveys generally cover the areas that adult sablefish inhabit, namely the upper continental slope. The longline surveys have occurred between early May and late September. The survey and fishery generally take place in the same area, the upper continental slope but the fishery generally takes place over a narrower depth range. Trawl surveys have also been conducted in Alaska, but compared with the longline surveys, they have not sampled as deeply and have covered fewer years. In stock assessments for Alaskan sablefish prior to 1996 (Fujioka, 1995; Lowe, 1995), the limited trawl data were used to convert relative abundance from the longline survey to absolute abundance by calibration to the trawl (Rose, 1986), and the population was modeled by using a delay-difference analysis (Kimura, 1985). The formulation of the delay-difference analysis applied to Alaskan sablefish was modified to provide annual recruitment estimates, with the assumption that trawl surveys measure absolute abundance (Fujioka, 1995; Lowe, 1995). The Alaskan sablefish stock assessment was like other Alaskan groundfish stock assessments, which historically have assumed that trawl surveys measure absolute abundance (Alverson and Pereyra, 1969). This assumption probably is wrong because fish can escape under the net (Engås and Godø, 1989a) and be herded by the bridles (Engås and Godø, 1989b). The motivation for the current study was to assess Alaskan sablefish without this assumption, relying only on longline survey estimates of relative abundance.

In the current study, I estimated absolute abundance for Alaskan sablefish with an age-structured population model, evaluated the estimation approach with Monte Carlo simulations, and investigated interactions of model parameters. Delay-difference analyses use annual abundance estimates and catches, whereas age-structured analyses additionally use annual

age or length data. The additional information allows explicit tracking of cohorts, but many more parameters must be estimated.

Fitting population models to survey and fishery data has long been used to estimate absolute abundance (Pope and Shepherd, 1985; Deriso et al., 1985) and is one method of estimating absolute abundance along with direct surveys, mark-recapture experiments and depletion experiments. Abundance estimation with a population model works by tracking population additions and losses and inferring absolute abundance from the manner in which catch affects the survey index and age and length compositions. In simple terms and aside from other losses, if harvesting 500 individuals decreases a cohort's index 10%, then the cohort's initial abundance was 5000 individuals. Estimation depends on having an abundance index precise enough to detect cohort reductions by the fishery.

The population model presented here takes into account the following unusual attributes of the available data. Length compositions are available from the longline surveys for all years analyzed, compared with infrequently available age compositions (Table 1). Not many Alaska-wide sablefish fishery data are available, consisting only of total catches and five years of fishery lengths, but no ages (Table 1).

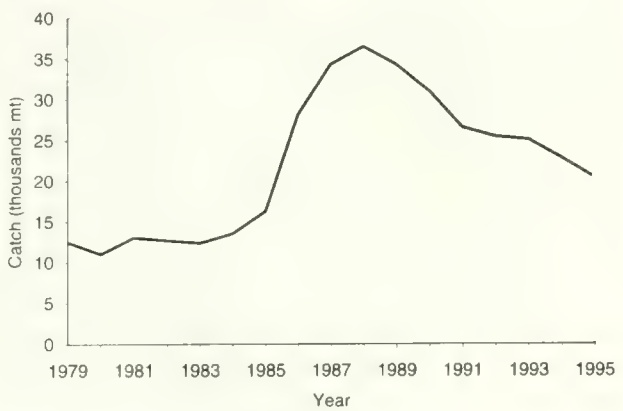

Figure 1

Reported fishery catches (thousands metric tons) from 1979 to 1995.

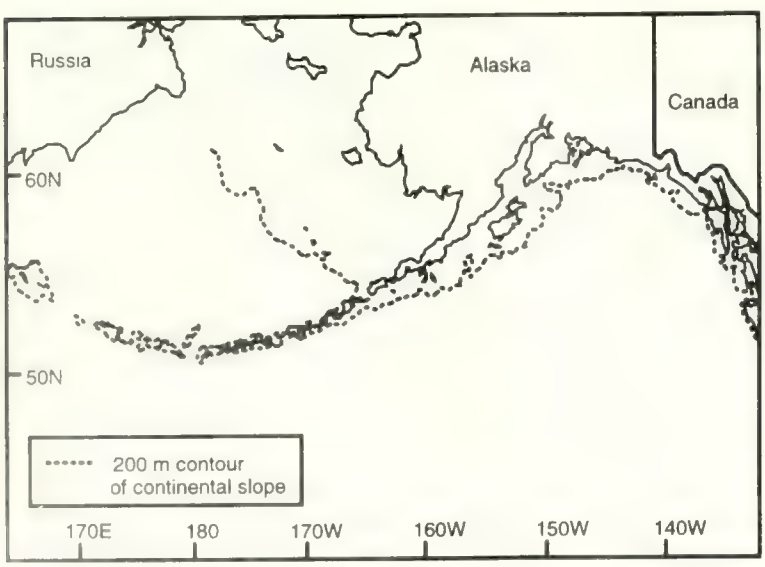

Figure 2

Map of southern Alaskan waters. Adult sablefish inhabit the upper continental slope seaward of the 200-m depth contour.

Methods

Model structure and estimation method

The analysis generally follows the approach described by Kimura (1990) for a separable age-structured population model. Let y, a, and l be the year, age, and length indices, respectively.

c_y = observed fishery catch in numbers;

I_y = observed survey abundance index in numbers;

p_{ya} = observed survey proportion at age;

p_{yl} = observed survey proportion at length;

$\mu_{ya} = \mu_y s_a$ = the exploitation fraction of age-a fish during year y which is separable into s_a, the selectivity for age-a fish, and μ_y, the exploitation fraction for fully vulnerable ages;

N_{ya} = the total number at age;

$N^f_{ya} = s_a N_{ya}$ = the exploitable (fishable) number at age; and

$\sum_a N^f_{ya} = N^f_y$ = the exploitable number.

Starting with initial cohort size, N_{ya}, natural deaths and observed catch were removed to compute next year's cohort size, $N_{y+1,a+1} = (1-\mu_{ya})\, N_{ya}\, e^{-M}$. A discrete fishery was modeled, $c_y = \mu_y N^f_y$, because the fishery was short for recent years except 1995. The modeled discrete fishery generally matches the timing of the observed discrete fishery and occurs near the mid-point of the earlier year-round fishery.

Table 1

Data sets used in the age-structured model of Alaskan sablefish. Length data are specified by sex.

Data component	Data aggregation	Years of data
Longline survey relative abundance	—	1979–95
Longline survey male lengths (cm FL)	40–41, 42–43, ..., 62–63, 64–69, 70–74, ..., 95–99	1979–95
Longline survey female lengths (cm FL)	40–41, 42–43, ..., 68–69, 70–74, 75–79, ..., 95–99	1979–95
Longline survey age	2, 3, 4, 5, 6, 7, 8, 9–10, 11–15, 16+ years	1983, 87, 89, 91, 93
Fishery total catch		1979–95

The modeled discrete fishery misrepresents the duration of the earlier year-round fishery, but tests with simulated data comparing a continuous fishery showed little difference in estimated abundance. The assumption of a discrete fishery simplified catch accounting and reduced model convergence time, which was important for the Monte Carlo simulations. This formulation limits the maximum exploitation rate for an age class to equal the selectivity for that age. This maximal rate would be achieved if the maximally selected age were completely harvested, with the exploitation rate equal to 1.0. This potential problem is not a real one because exploitation rates never approach such high levels for Alaskan sablefish.

Selectivity was described by the "exponential-logistic" function (Thompson, 1994),

$$s_a = \left(\frac{1}{1-\gamma}\right)\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{e^{\beta\gamma(A_{50}-a)}}{1+e^{\beta(A_{50}-a)}}\right).$$

The "exponential-logistic" function is flexible, allowing both asymptotic selectivity when selectivity increases with age to an asymptote, and dome-shaped selectivity when selectivity increases with age to a maximum, then decreases for older fish. The exponential-logistic function automatically scales maximum selectivity to 1.0 and reduces to asymptotic selectivity as the parameter gamma (γ) approaches zero. When $\gamma = 0$, the parameter A_{50} is the age where 50% of the population is vulnerable and β is the slope of the function at A_{50}. When $\gamma > 0$, then A_{50} and β lose their biological meaning, because A_{50} no longer represents the age at 50% vulnerability. Selectivity is assumed equal for the fishery and survey. Both the fishery and survey mostly use longline gear and cover the same area. Their similar length frequencies support this assumption (Fig. 3). The fishery length data were not incorporated into the model because of this similarity and because few years of fishery length data were available.

Age data were aggregated over adjacent ages (Table 1) as suggested by Deriso et al. (1989) because sablefish are difficult to age, especially those older than eight years (Table 6 in Kimura and Lyons, 1991). Ages greater than eight years were not pooled into a single class because females continue to grow, though slowly, after eight years. This growth information was needed in the model to convert ages to lengths. Length data also were aggregated (Table 1). Another way to deal with ageing error is to include a matrix of misageing probabilities in the age-structured model (Kimura, 1990), but this approach was not used because the misageing probabilities were unknown.

Estimated data values were computed from the parameter estimates. The estimated abundance index is $\hat{I}_y = \hat{q}\hat{N}^f_y$, where q is survey catchability. Quantities estimated from this model and used in the model fitting algorithm are denoted with "hats." The estimated age compositions are

$$\hat{p}_{ya} = \frac{\hat{N}^f_{ya}}{\sum_a \hat{N}^f_{ya}}.$$

An age-length transition matrix, $L = (l_{al})$, also was calculated from the survey age data, where l_{al} is the probability that a sampled fish of age a will be of length l. The age-length transition matrix is assumed constant over time. Probabilities were computed by region and year, then pooled as an average weighted by sample size. Estimated age compositions were converted to estimated length compositions with the age-length transition matrix,

$$\hat{p}_{yl} = \sum_a \hat{p}_{ya} l_{al}.$$

The parameters were estimated by maximum likelihood by assuming multinomial errors for age and length data and log-normal errors for catch data (Fournier and Archibald, 1982) and by using the quasi-Newton algorithm implemented in Microsoft Excel. Assuming that the effective sample sizes are the same for age and length samples and that the

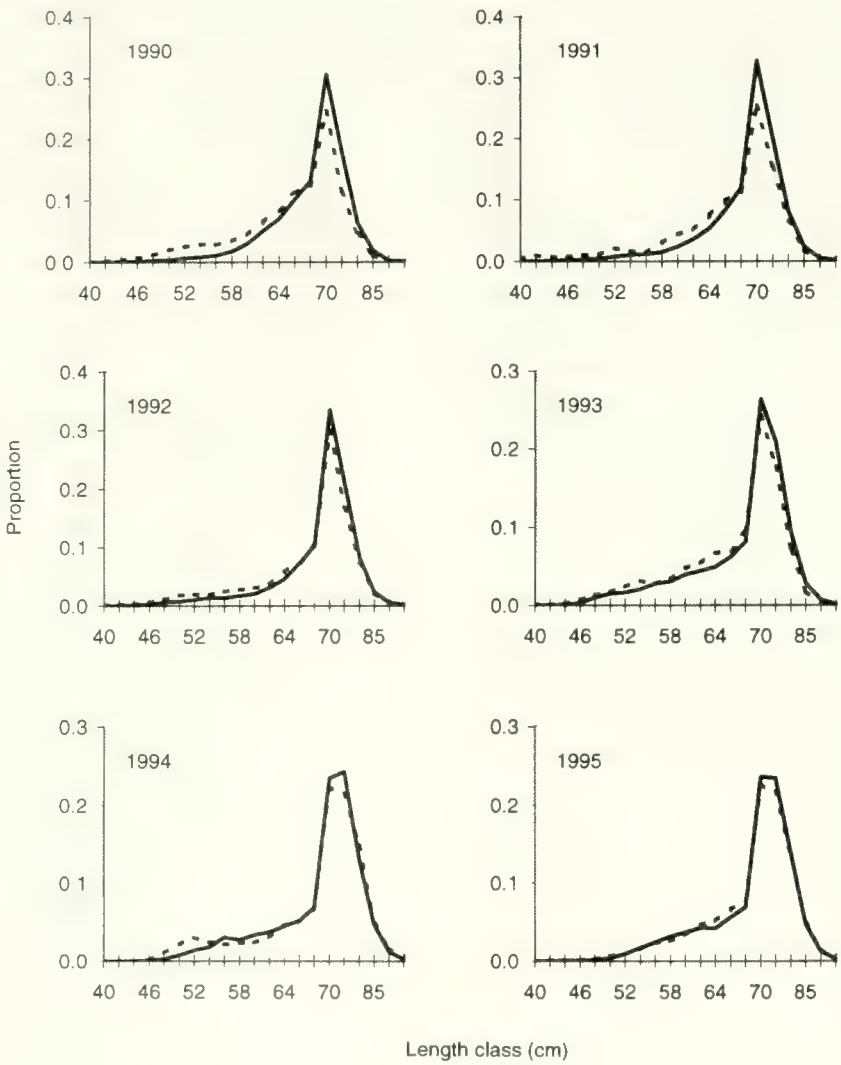

Figure 3

Survey (——) and fishery (– – –) length compositions for females. Male lengths also are available, but only female lengths are displayed for brevity. Alaska-wide fishery length data were available only since 1990.

age and length samples are independent, then the log-likelihood is

$$L = \sum_{ya} p_{ya} \log \frac{\hat{p}_{ya}}{p_{ya}} + \sum_{yl} p_{yl} \log \frac{\hat{p}_{yl}}{p_{yl}}$$

$$-\lambda \sum_{y} \left(\log(I_y) - \log(\hat{q}\hat{N}_y^f) \right)^2 + \text{constant},$$

where λ is the ratio of the effective multinomial sample sizes, either age or length, to the variance of the log-transformed abundance index (Deriso et al., 1985). Thus λ is a weighting factor that adjusts the relative influence of the abundance index and age and length components of the likelihood. The range of λ from 0.02 to 10 was tested. The value $\lambda = 1$ appeared the most reasonable and is used henceforth. This value was chosen on the basis of fit of each data type and the effect on the estimated recruitment values as λ was varied. As λ increased from 0.02 to 10, the fit of the index data improved only at the expense of the fit of the length data, but the relative sizes of the annual recruitment estimates were unaffected for $\lambda < 2$. Increasing λ substantially improved the fit of the index data until λ was from 1 to 2, when improvement slowed. Thus a value of λ between 1 and 2 seems reasonable, with $\lambda = 1$ chosen because the fit of the age data was best at that point. In prac-

tice, $\lambda = 1$ implies an effective sample size for the age and length samples of 100 if the CV of the survey index is 10%. This CV is reasonable according to a statistical analysis of the survey index, which found that a 10% interannual change in the survey index typically was statistically significant at the $P = 0.05$ level (Sigler and Fujioka, 1988). The reasonableness of the effective sample size is harder to determine because the age and length samples are composites of multinomial samples from survey stations with underlying geographic variation in age and length compositions, so that the effective sample size is less than the true sample size. In the above expression $\log(\hat{p}_{ya})$ usually found in the log-likelihood for the multinomial distribution was replaced with $\log(\hat{p}_{ya}/p_{ya})$. This replacement removes a "nonsignificant" portion of the likelihood and makes it easier to examine the model fit and probably somewhat improves numerical performance (Kimura, 1990).

Assuming M and λ are known, this model contains $Y + A + 2$ parameters: recruitment, $N_{11}, \ldots, N_{Y1}$, the initial age composition, $N\hat{q}_{12}, \ldots, N_{1A}$, and the selectivity parameters, A_{50}, β, and γ are unknown. The quantities and $\hat{\mu}_1, \ldots, \hat{\mu}_Y$ are functions of the observed survey indices and observed catches and of the parameter estimates. Setting dL/dq equal to zero and solving for q gives

$$\hat{q} = \exp\left[\frac{\sum_y \log \frac{I_y}{\hat{N}_y^f}}{Y}\right].$$

The $\hat{\mu}_1, \ldots, \hat{\mu}_Y$ are computed from $\hat{\mu}_\gamma$

$$= \frac{c_y}{\hat{N}_y^f},$$

by treating reported catches as exact. Although clearly there will always be some error in the reported catch, I concluded that this approximation generally was reasonable given the comprehensive system for tracking the Alaskan sablefish catch, which includes processor reports, fish receipts, individual fishing quota landing reports, and observer coverage. I estimated log-parameters rather than parameters on the original scale to improve reliability in the estimation process (Kimura, 1989, 1990).

An allowable biological catch (ABC_{96}) was calculated from a 1-year future projection. The constant fishing mortality, $F_{40\%}$, was applied, which reduces the exploitable population to 40% of the unexploited state (Clark, 1991). A 1-year projection of recruitment was forecast as the average of recent estimated recruitments. The two most recent recruitments were not used in the average; their estimates, based on only one or two years of data, are unreliable.

Validation of estimation method

I used Monte Carlo simulation for model validation (Kimura, 1989; Press et al., 1989) to verify that the age-structured analysis provides reasonable results. The steps (Press et al., 1989) are as follows: 1) Fit the model using real data; 2) take the estimated parameter values as the true values for the simulation; 3) calculate the expected data based on these parameter values, then simulate a new data set by adding a particular error to the expected data based on an observed mean square error (MSE) or any hypothetical value; and 4) estimate the model parameters for the simulated data. If the resulting parameter estimates and the true parameter values are similar, then the estimation method is to some extent validated. This approach assumes that the model fits the simulated data perfectly except for random error. If the true errors were of larger magnitude or arose from a different source than that assumed in fitting the model, for example in violating the assumptions of equal fishery and survey selectivity and constant growth rates, then estimation performance with simulated data overstates the true model performance.

Log-normal error (CV=0.10 on the original scale) was added to the expected abundance index, and multinomial error (n=200) was added to the expected age and length data. These values were based on variability of the model residuals (difference between the observed and expected data). The log-transformed abundance indices are assumed to be independent, normally distributed random variables, and a "minor dilemma" (Kimura, 1989) arises on whether to simulate the abundance indices so that they are unbiased on the original or the logarithmic scale. I chose to simulate the abundance indices so that the survey index was unbiased on the original scale.

Age data are often limited in availability, whereas length data are nearly always available. Age data are more desirable than length data for estimating age structure because the correspondence between age and length is not one-to-one. Age data are commonly inaccurate: some individuals, especially older fish, are misassigned to ages around the true age. Thus, inaccurate age data and length data are similar in that true age does not uniquely correspond to assigned age or length. Parameters were estimated from simulated data for both accurate and inaccurate age data, the latter also being equivalent to length data. For accurate age data, 100% of fish of simulated samples were correctly assigned and cat-

egorized as {2, 3, ..., 15, 16+} . For inaccurate age or length data, 50% were correctly assigned to the true age, 20% to –1 year, 20% to +1 year, 5% to –2 years, and 5% to +2 years, then categorized as {2, 3, ..., 8, 9+} .

Survey selectivity may affect parameter estimation. Bence et al. (1993) found that biomass estimates were more accurate and precise for a population model with data from a survey with asymptotic selectivity than from one with dome-shaped selectivity. Therefore, both asymptotic and dome-shaped selectivity were compared. The dome-shape was chosen such that the availability of the last age group was 0.5.

A measure of the variability of biomass estimated in the simulations is the MSE computed from parameter estimates and their "true" values. Mean square error (MSE) was converted to coefficient of error (CE), defined as the "true" value divided into the square root of MSE (Kimura, 1990). Twenty-five to fifty replicate simulations were completed for each scenario.

Results

Model results for the original data

The model fitted all the original data well: abundance index (Fig. 4), age data (Fig. 5), and length data (Fig. 6). The estimate of survey catchability appears good; the likelihood profiled over a range of catchabilities shows a distinct, regular curvature (Fig. 7). Estimated exploitable biomass for 1995 was 181,000 t (Fig. 8), and projected ABC_{96} was 19,600 t. Estimated biomass decreased from a peak in the mid-1980s. The peak is attributed to strong recruitment in the late 1970s; recruitment has decreased in recent years (Fig. 9). Estimates of recent exploitation rates for fully selected ages average 10% (Fig. 8), which is near the exploitation rate equivalent to $F_{40\%}$, the current reference point for sablefish management in Alaska. The shape of the estimated selectivity curve was asymptotic (i.e. γ=0).

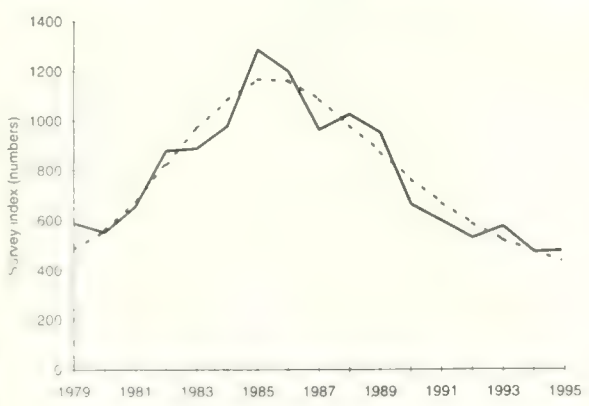

Figure 4

Observed (——) and expected (– – –) survey index (numbers) from 1979 to 1995.

The estimate of natural mortality for sablefish is uncertain; therefore its effect on abundance estimation was examined. An important part of this examination was to analyze the interaction between M and other key parameters. Model parameters were estimated for several fixed values of natural mortality around M = 0.10 (Table 2). The log-likelihood is not maximized at M = 0.10, and there is a slightly higher value for M = 0.12 (panel 1). Catchability was smaller and exploitable biomass was larger for larger M (panel 2); biomass was larger to account for more natural deaths. The fishable fraction of the total population

$$\left(\sum_a s_a N_{ya} \Big/ \sum_a N_{ya} \right)$$

was smaller for larger M (panel 3) because the fish recruited later (panel 4). Asymptotic selectivity was estimated whatever the value of M (panel 5). ABC_{96} was larger for larger M (panel 6) because exploitable biomass was larger and the fishing rate, $F_{40\%}$, increases with M.

Natural mortality and survey catchability can affect abundance estimates; therefore their effect was examined. Model parameters were estimated for several fixed values of q and M (Table 2). For each fixed M, the approach was to fix q at values near the estimated q. The results are likelihood profiles of q for each fixed M (panel 1). Given M, exploitable biomass was smaller for larger q (panel 2). The effect of q on the fishable fraction was more complicated. Given M, the fishable fraction was smaller for the fixed q that was less than the estimated q (panel 3) because older fish were less vulnerable to the fishery (panel 5). Given M, the fishable fraction was less for the fixed q that was greater than the estimated q because fish recruited later (panel 4). Selectivity was asymptotic and could not increase above 1.0, forcing the decreased fishable fraction to occur by means of a later recruitment age. ABC_{96} was larger for smaller values of q (panel 6) because exploitable biomass was larger (panel 2).

Model results for the simulated data

Biomass estimates were unbiased for simulations based on a survey with asymptotic selectivity, when

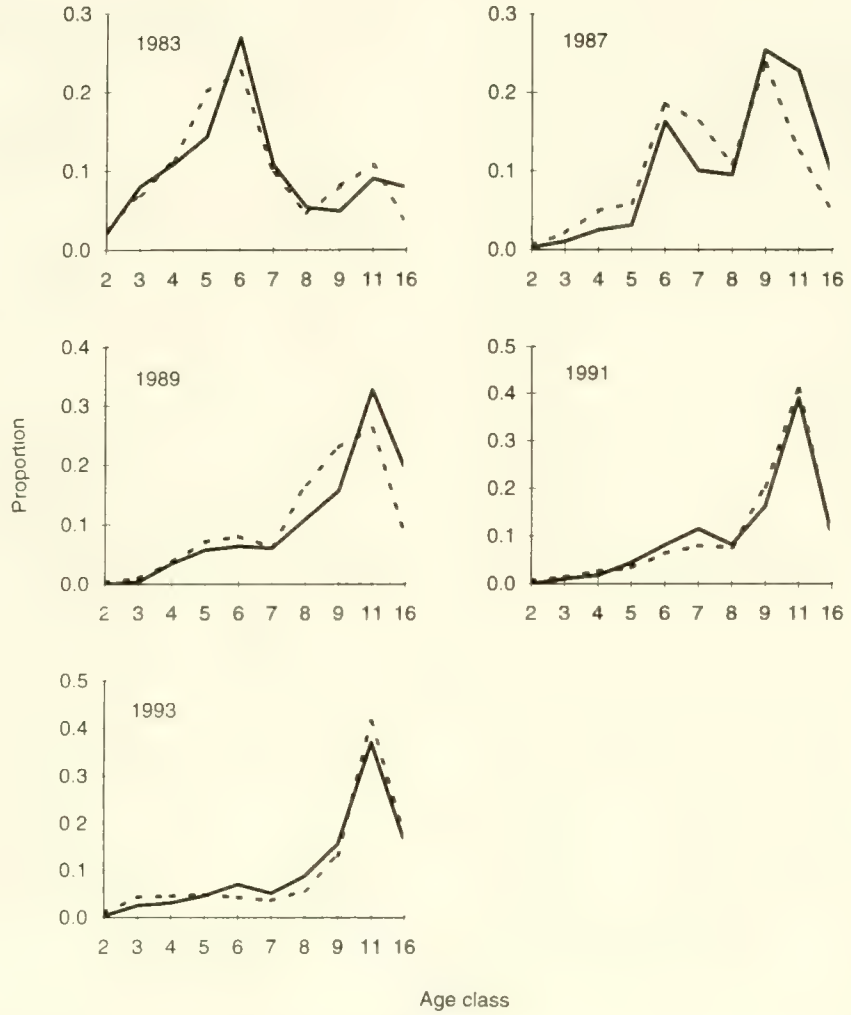

Figure 5

Observed (——) and expected (– – –) age compositions. Data were available only from the 1983, 1987, 1989, 1991, and 1993 surveys. See Table 1 for age-class definitions.

age and length data were used (Fig. 10A). Estimated error (CE [exploitable biomass]) was about 0.08, increasing for the later years to about 0.12 (Fig. 11), values similar to the assumed CV for the abundance index of 0.10. These values all imply that sablefish abundance could be estimated given the type and quality of data assumed in these simulations. These simulations match my evaluation of the actual data. Biomass estimates also were unbiased for asymptotic selectivity, no matter whether age or "length" data were used (Fig. 10, B and C); CE (exploitable biomass) ranged from 0.10 to 0.15 (Fig. 11). In contrast, biomass estimates were positively biased by 14% to 17% for dome-shaped selectivity (Fig. 10D) and CE (exploitable biomass) ranged from 0.40 to 0.50 (Fig. 11). Thus, estimating abundance from a survey with asymptotic selectivity appears reasonable; biomass estimates derived from a survey with dome-shaped selectivity can be estimated, but may be biased and less precise.

Discussion

Comparison of age-structured and delay-difference analyses

The estimates of sablefish exploitable biomass from age-structured analysis and delay-difference analysis are similar (Fig. 12). Both analyses show exploitable biomass rising from about 170,000 t in 1979, peaking at about 420,000 t around 1986, and falling since then to about 200,000 t in 1995. The trend from the sablefish delay-difference analysis is less smooth

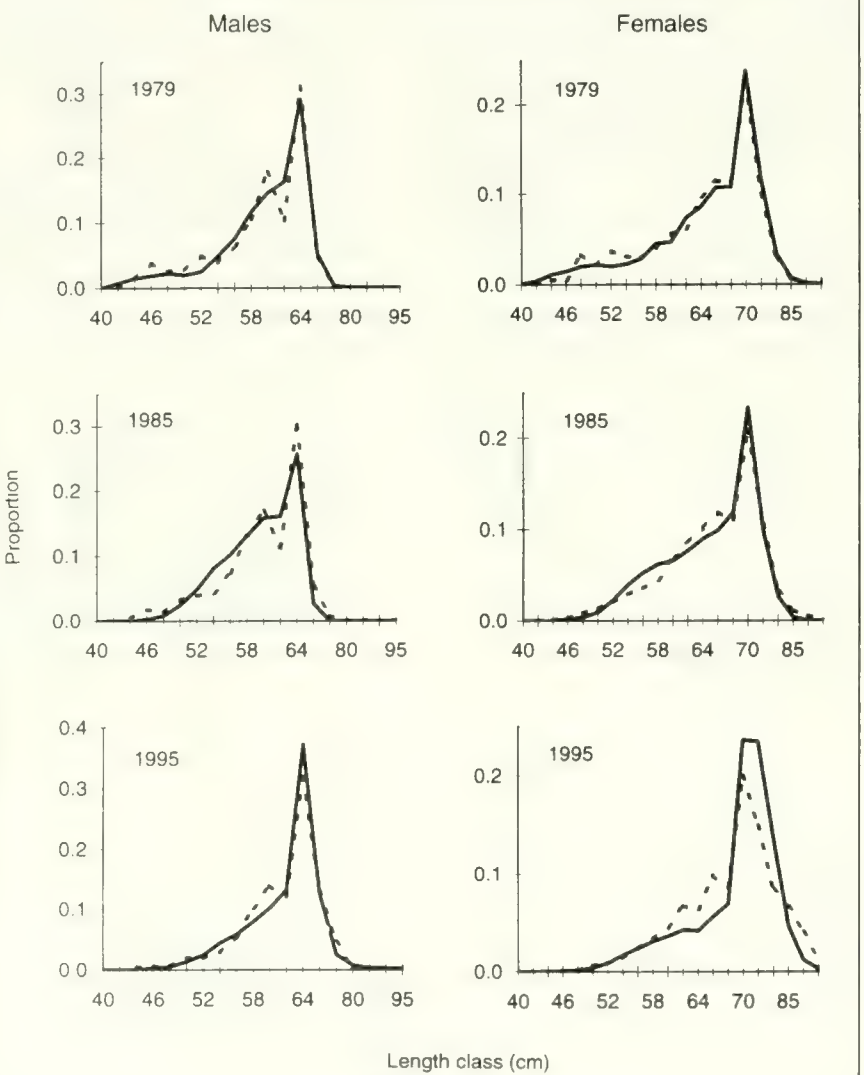

Figure 6

Observed (——) and expected (– – –) length compositions. Data were collected during all annual surveys from 1979 to 1995, but only a subset is displayed for brevity. See Table 1 for length-class definitions.

because the estimates are linear functions of the survey abundance index. Exploitable biomass follows every up and down in the abundance index. All measurement error is reflected in the recruitment estimate. The trend from the age-structured analysis is a complicated function of the abundance index and the age and length data and smooths annual changes in the abundance index.

The simulations in this paper imply that the age-structured model provides reliable estimates of sablefish absolute biomass. The assumption that trawl surveys provide absolute biomass estimates required for the sablefish delay-difference analysis can be dropped. Starting with the 1997 fishing year, the age-structured analysis has supplanted the delay-difference analysis in the stock assessment for estimating biomass(Fujioka et al., 1996).

Comparison to other estimates of sablefish abundance

Sablefish absolute abundance was estimated in two other studies, but the estimates were unreasonable. Sablefish longline catchability was estimated by depletion experiments (Clausen et al., 1997). The computed longline catchabilities were applied to the sablefish longline survey results for the Gulf of Alaska; the resultant biomass estimates of 50,000–

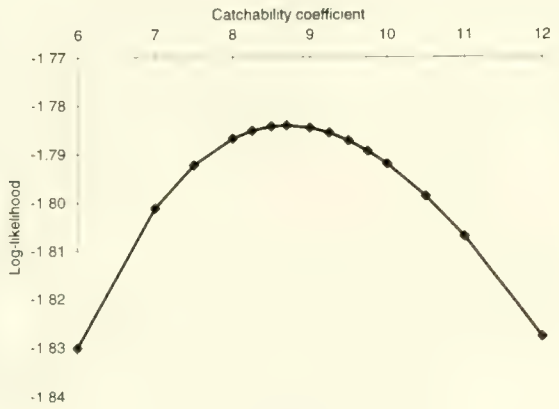

Figure 7

Log-likelihood versus catchability coefficient.

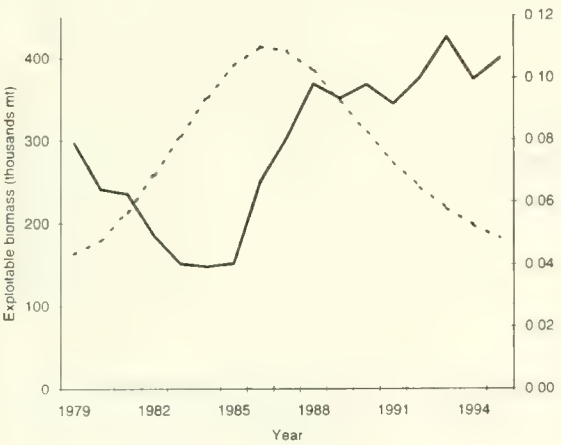

Figure 8

Estimated exploitable biomass (– – – , thousands metric tons) and exploitation rate (——) versus year.

60,000 t were unreasonably low because during the same period, the longline relative abundance index was stable even though annual commercial catches were 20,000–30,000 t (Clausen et al., 1997).

Eggers et al. (1982) described a quantitative method of estimating the effective radius of a baited hook or pot by comparing catch rates between gear with different spacings between baits. They applied this method to a hook-spacing experiment for sablefish longline gear and estimated that the bottom area fished per hook was 4.8 m^2. I applied this estimate to the time series of longline relative abundance indices, which implied that sablefish absolute biomass in Alaska ranged from 7 to 16 million t during 1979 to 1996, a range that seems improbably high because catches of about 50,000 t in the early 1970s subse-

Table 2

Log-likelihood, estimated values of exploitable biomass (thousands metric tons, age 2+) for 1995, the fishable fraction of the total population in numbers for 1995, age at 50% vulnerability, vulnerability of the last age class (s_{term}, where $s_{term} < 1$ implies a dome-shaped selectivity function), and projected allowable biological catch for 1996 (ABC_{96}). Values were estimated from the original data. Log-likelihood is the value of the objective function. Selectivity, recruitment, and initial age composition always were estimated. Asterisk (*) indicates results where survey catchability was estimated and natural mortality was fixed. No * indicates results where survey catchability and natural mortality were fixed.

Catchability coefficient	Natural mortality (M)				
q	0.05	0.08	0.10	0.12	0.15
Log-likelihood					
4.17				–1.781	–1.757*
6.85			–1.795	–1.770*	–1.789
8.70		–1.817	–1.784*	–1.786	
10.61	–1.869	–1.802*	–1.801		
13.59	–1.834*	–1.837			
Exploitable biomass					
4.17				366	362*
6.85		229	226*	215	
8.70		184	181*	175	
10.61	152	151*	146		
13.59	121*	115			
Fishable fraction					
4.17				0.735	0.821*
6.85			0.770	0.826*	0.789
8.70		0.772	0.830*	0.806	
10.61	0.673	0.833*	0.809		
13.59	0.837*	0.801			
Age at 50% availability					
4.17				4.0	4.2*
6.85			4.0	4.1*	4.6
8.70		3.9	4.0*	4.4	
10.61	4.0	4.0*	4.3		
13.59	3.9*	4.5			
s_{term}					
4.17				0.70	1.00*
6.85			0.78	1.00*	1.00
8.70		0.78	1.00*	1.00	
10.61	0.52	1.00*	1.00		
13.59	1.00*	1.00			
ABC_{96}					
4.17				68.5	62.9*
6.85			33.4	30.2*	39.0
8.70		22.7	19.6*	24.0	
10.61	23.0	12.8*	16.2		
13.59	6.4*	10.1			

quently resulted in sharp declines in fishery catch rate (Fujioka, 1986; McDevitt, 1986).

An estimate of the area occupied by adult sablefish was used to calculate the depletion and hook-spacing estimates of absolute biomass. The estimated area is inexact and, correspondingly, so are these biomass estimates. However this area would have to be an order of magnitude higher or lower to be consistent with the observed catch effects on the abundance indices, a level of error unlikely given the extensive longline surveys for sablefish.

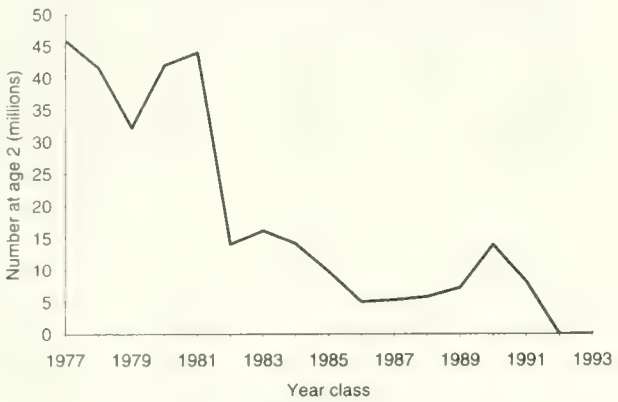

Figure 9

Number at age 2 (millions) versus year class.

Data and model requirements necessary to estimate abundance

Estimates of absolute abundance for sablefish were unbiased (Fig. 10, A–C) and relatively precise (Fig. 11) when selectivity was asymptotic. Abundance estimates were relatively precise regardless of whether age data alone, length data alone, or age and length data together were used. Even though length data alone is less desirable than age data for estimating annual recruitment, the precision of the abundance estimates was similar, supporting the notion that length data is useful for abundance estimation with age-structured analyses.

Dome-shaped selectivity affects abundance estimation. Sablefish abundance estimates were positively biased (Fig. 10D) and less precise (Fig. 11) for a survey with dome-shaped selectivity. Abundance estimates for a simulated widow rockfish, *Sebastes entomelas*, fishery off the western coast of the continental United States also were less accurate and less precise for a survey with dome-shaped selectivity than one with asymptotic selectivity (Bence et al., 1993). Thus, surveys with asymptotic selectivity appear better for abundance estimation than surveys with dome-shaped selectivity.

The sablefish age-structured model was fitted with 17 years of survey length data, but only five years of survey age data and no fishery age or length data. Two assumptions probably were the keys to how it was possible to fit an age-structured model with only limited age data (Table 1). One key assumption is that selectivity is equal for the fishery and survey, so that no fishery age or length data were required to independently estimate fishery selectivity. Another key assumption is that the age-length transition matrix is constant over time, so that

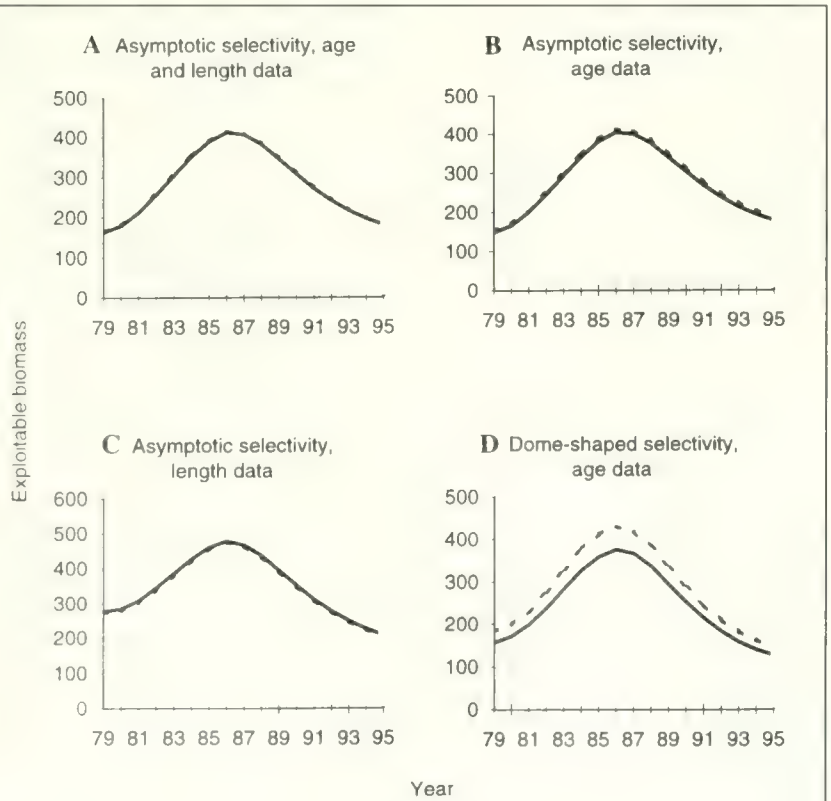

Figure 10

Exploitable biomass (thousands metric tons) versus year for simulated data. The "true" values (——) are compared with the average values (– – –) for the simulations.

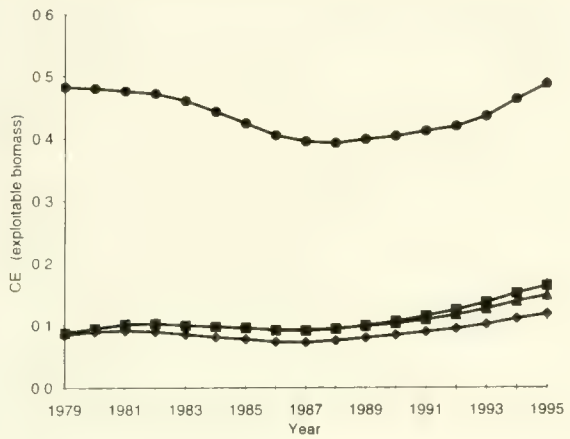

Figure 11

Coefficient of error (CE) of the exploitable biomass (thousands metric tons) versus year: asymptotic selectivity, age and length data (◆); asymptotic selectivity, age data (■); asymptotic selectivity, length data (▲); and dome-shaped selectivity, length data (●).

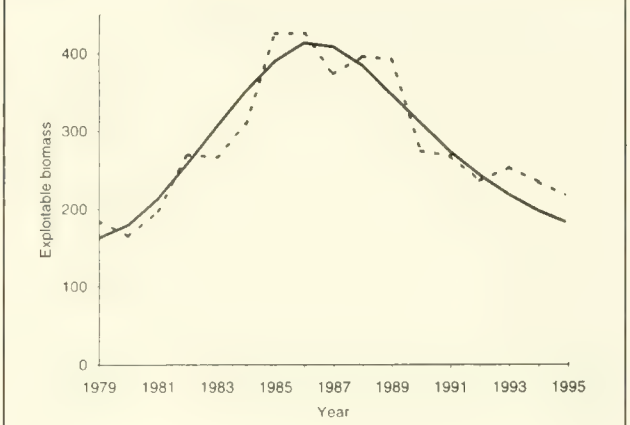

Figure 12

Estimates of exploitable biomass (thousands metric tons) by delay-difference analysis (– – –) and age-structured analysis (——).

age structure could be inferred from survey length data for the several years where no age data were available. This latter assumption may hold for sablefish, but would be conspicuously violated for other species such as Pacific halibut, *Hippoglossus stenolepis*, whose growth rate has changed over time. Recent improvements in Alaskan sablefish data collection eventually will lead to tests of these assumptions. Otoliths have been collected and read annually from longline surveys since 1995. Fishery lengths have been collected annually since 1990.

A measure of relative abundance, effort data, was necessary to obtain reasonable estimates of absolute abundance with an age-structured model of Pacific halibut, as shown by comparison to cohort analysis of historical data of year classes with complete catch data (Deriso et al., 1985). The frequency and number of the relative abundance estimates can affect abundance estimation. Absolute biomass was estimated successfully for Alaskan sablefish in this paper and for the simulated widow rockfish fishery (Bence et al., 1993). Annual surveys were simulated for 17 and 15 years, respectively. However, precise abundance estimates may not always be possible when survey effort is less. Three triennial surveys were insufficient to estimate absolute abundance for the eastern Bering Sea walleye pollock fishery with useful precision (Kimura, 1989). Species-specific simulations can help to determine the amount of survey effort necessary to estimate absolute abundance. For example, McAllister (1995) examined survey timing for assessments of the eastern Bering Sea yellowfin sole fishery. A population dynamics model was fitted to two survey time series, 1975–81 and 1982–94, then the population was projected forward 15 years and annual, versus triennial, trawl surveys were compared. Net present value of the fishery was less for more frequent surveys, primarily owing to increased survey cost, but CV (*ABC*) was less for more frequent surveys (28 versus 36%) when absolute abundance was estimated.

Parameter interactions with abundance estimates

Abundance estimates are related to estimates of several model parameters. Absolute abundance and survey catchability are inversely related because a given observation of the survey abundance index can be due to a small population that is easy to catch or to a large population that is difficult to catch. Natural mortality and catchability also are inversely related; increasing q while decreasing M tends to give similar log-likelihood values (Table 2, panel 1). Absolute abundance and natural mortality tend to be positively correlated (panel 2; Schnute and Richards, 1995). Given the observed abundance index, absolute abundance estimates must be larger for the population to sustain more natural mortality. Reducing the correlation and improving estimation of natural mortality is difficult because the number of natural deaths for marine fish species is usually unobservable; no data are available to estimate M directly. For the sablefish age-structured analysis, the overall changes in the likelihood function with respect to M were minor and not sufficient to allow estimation of M as part of the model-fitting process. I had to fix

M outside the model at the "best," most reasonable value, then estimate absolute abundance with the population model.

The likelihood surface was mapped to examine the parameter relationship between q and M (Table 2, panel 1). I found it useful to fix one parameter, then estimate the other parameter, thus ensuring that the peak of the likelihood ridge as a function of q and M was found. An alternate, seemingly useful approach is a grid over fixed values of q and M. I do not recommend this approach. It is difficult and time consuming to design a grid fine enough and large enough to map the peak of the likelihood ridge. In earlier modeling, not described in this paper, this approach led me to declare incorrectly a global minimum over q and M because the grid was too coarse and the likelihood ridge poorly mapped.

Thompson (1994) demonstrated analytically that M and the degree of curvature of dome-shape are confounded because fish may "disappear" with age, owing to natural death or decreased vulnerability. Survey catchability and selectivity also were confounded (Table 2, panel 3). Fish recruited later (panel 4) or were less vulnerable when older (panel 5), depending on the value of survey catchability. Older fish were less vulnerable when fixed q was less than estimated q (panel 5).

The lower vulnerability of older fish for lower catchability values is a clue as to why abundance estimation is less reliable when selectivity is dome-shaped. Absolute biomass is inferred in the model from how the catches affect the survey index, as described in the introduction, and this effect implies some specific estimate for absolute abundance. Older fish were less vulnerable to compensate for lower survey catchability, which helps to maintain the absolute biomass estimate implied by the catch and survey index. Estimated biomass is similar with either higher catchability or lower vulnerability of older fish, i.e. greater degree of curvature of dome-shape. This parameter interaction probably is why abundance estimation is more difficult when selectivity is dome-shaped.

In some cases, selectivity can be estimated independently to eliminate the problem of confounding parameters with selectivity. If a species is surveyed by two overlapping surveys and gear selectivity is known for one survey, then the unknown gear selectivity can be estimated by comparing the survey length compositions (Kimura, 1978). This approach helps to estimate gear selectivity, but not to estimate availability with age, where availability at age is the fraction of the population within the survey area by age. Modeling availability at age will depend on survey coverage in relation to ontogenetic changes in spatial distribution.

The age-structured model presented here is a tool for interpreting the data collected from the sablefish fishery and longline survey. Simulations and an examination of parameter relationships help one to understand how the tool performs, its reliability, and its strengths and weaknesses. The population model appears reliable for interpreting the sablefish data and has been adopted for estimating abundance and setting quotas for sablefish management. The conclusions regarding data and model requirements for estimating abundance and parameter interactions with abundance estimates should be generally applicable to other species. The sablefish age-structured model is like other north Pacific age-structured models except for the assumption of a discrete fishery. In one respect, these simulations were a more difficult test of an age-structured model to estimate abundance because one scenario examined length data alone, an imprecise measure of age structure.

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Fisheries benefits and optimal design of marine reserves

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Abstract.—We used fishery population models to assess the potential for marine fishery reserves, areas permanently closed to fishing, to enhance long-term fishery yields. Our models included detailed life history data. They also included the key assumptions that adults did not cross reserve boundaries and that larvae mixed thoroughly across the boundary but were retained sufficiently to produce a stock-recruitment relationship for the management area. We analyzed the results of these models to determine how reserve size, fishing mortality, and life history traits, particularly population growth potential, affected the fisheries benefits from reserves. We predict that reserves will enhance catches from any overfished population that meets our assumptions, particularly heavily overfished populations with low population growth potential. We further predict that reserves can enhance catches when they make up 40% or more of fisheries management areas, significantly higher proportions than are typical of existing reserve systems. Finally, we predict that reserves in systems that meet our assumptions will reduce annual catch variation in surrounding fishing grounds. The fisheries benefits and optimal design of marine reserves in any situation depended on the life history of the species of interest as well as its rate of fishing mortality. However, the generality of our results across a range of species suggest that marine reserves are a viable fisheries management alternative.

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Fishing activity impacts the marine environment in several ways. Individual species risk severe declines from overexploitation. Over two-thirds of all fisheries world-wide are classified as fished beyond capacity or in danger of becoming so (FAO, 1995), and higher trophic levels are particularly affected (Pauly et al., 1998). Along with target species, fishing can reduce the populations of nontarget species that are caught and discarded. The ecosystems that support the fisheries also face risks. Fishing can cause biological damage to ecosystems when the reduction of key species or trophic levels causes ecological shifts (e.g. Hay, 1984; Castilla and Durán, 1985; Hay and Taylor, 1985; Durán and Castilla, 1989; McClanahan and Shafir, 1990; Roberts, 1995; McClanahan et al., 1996; Pauly et al., 1998). Fishing can also cause physical damage to ecosystems, particularly when dwindling fish catches promote the incentive to use damaging fishing practices (McAllister, 1988).

Reserves can protect the ecosystems within them from damaging fishing practices and have the potential to reestablish a natural ecosystem balance (Russ, 1985; Plan Development Team, 1990; Roberts and Polunin, 1991; Dugan and Davis, 1993; Roberts and Polunin, 1993; Rowley, 1994; Roberts et al., 1995; Bohnsack, 1996). Field studies have generally demonstrated that fish stocks build up within a protected area (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1994; Bohnsack, 1996, and references within) but much less information exists on fishery enhancements.

In theory, reserves can maintain productive fisheries by protecting a critical stock within their borders. These stocks may enhance catches through adults that grow larger in the reserve and then migrate to fishing areas (adult spillover), or through enhanced recruitment in fishing areas due to increased population fecundity from the reserve (larval transport). In practice, fisheries benefits from reserves have rarely been demonstrated or even measured. This lack of field evidence reflects the difficulty of performing controlled and replicated experiments in unpredictable political and biological systems.

The few existing field studies addressing fisheries benefits from reserves show promise. A marine fishery reserve encompassing over 60% of the former fishing grounds north of Mombasa, Kenya, showed a 110% increase in catch per unit of effort after only two years (McClanahan and Kaunda-Arara, 1996). Total catches had not yet met those prior to reserve establishment, but trends looked favorable. On Apo Island, Philippines, total fish density and

species richness had increased by over 400% in both the reserve and the fishing grounds after 11 years of reserve protection (Russ and Alcala, 1996). Large fish were particularly abundant in the fishing grounds near the border of the reserve, possible evidence of adult spillover. These same authors showed previously that overall catches dropped more than 50% two years after the re-opening of a closed area on Sumilon Island, Philippines, despite the increased fishing area (Alcala and Russ, 1990), suggesting that the reserve had provided enhancements to surrounding fishing grounds.

These field studies show that under certain circumstances, reserves are likely to produce fisheries enhancements. However, models are also necessary because they allow more general analyses of the conditions under which reserves are likely to produce benefits and of the design attributes that will maximize these benefits. By making use of controlled replicates and large-scale manipulations, models can provide a theoretical background on which to interpret field results.

Several authors have built and analyzed models of marine fishery reserves. These models can be classified as those examining adult spillover (Beverton and Holt, 1957; Polacheck, 1990; DeMartini, 1993) and those examining larval transport (Quinn et al., 1993; Man et al., 1995; Holland and Brazee, 1996; Sladek Nowlis and Roberts, 1997; Holland et al.[1]). All of these models predict fisheries enhancements from reserves in at least some situations, particularly under heavy exploitation. However, the predicted enhancements were small and uncommon for the adult spillover models. Previous models have examined a variety of factors that influence potential reserve benefits, including adult movement tendencies (Polacheck, 1990; DeMartini, 1993), individual growth rate (DeMartini, 1993), Allee effects (Quinn et al., 1993), metapopulation patch dynamics (Man et al., 1995), and socioeconomic factors (Holland and Brazee, 1996; Holland et al.[1]). None of these examined the effect of population growth potential on reserve benefits.

In order to fill this gap, we built a set of models looking at reproductive enhancement and larval transport as mechanisms for providing reserve benefits. We analyzed these models with particular emphasis on how reserve size, fishing mortality, and life history traits, particularly population growth potential, affect long-term fishery yields. We also analyzed the short-term consequences of reserve establishment and these results are presented elsewhere (Sladek Nowlis and Roberts, 1997).

We used our models to achieve several goals. First, we wanted to identify conditions that favored the success of reserves at enhancing fisheries. Second, we wanted to establish design criteria to help maximize the benefits that could accrue from a closed fishing area. Third, we wanted to assess whether reserves can decrease year-to-year variation in catches. Finally, we wanted to provide guidelines for future field research through the identification of important but poorly understood biological processes and through the generation of testable predictions about the design and function of marine fishery reserves.

Methods

Our basic model followed yearly changes in a population separated into size categories. Although categorization by age is more common than by size, we felt size better represented size-dependent processes such as reproduction and fishing mortality (Polunin and Roberts, 1996). Each size category contributed to future populations through some simple rules (Fig. 1).

We used the best-available estimates of size-based fecundity and larval survivorship for various species (see Table 1). Little is known about larval survivorship in fish, especially for coral reef species (Boehlert, 1996). The best estimates we could find came from an analysis of larval performance across a global array of ambient temperatures (Houde, 1989). Houde used linear regression on data from various studies to relate ambient temperature to fish larval duration and daily survivorship. This process produced statistically significant and predictive, but crude, relationships that could then be combined to estimate total larval survivorship. At a temperature of 26°C, Houde's estimate of survivorship for larvae through the entire larval stage was 5×10^{-5} (see Appendix for equations). Whenever we had additional information about larval stage duration, we used it along with Houde's temperature-based estimate for daily survivorship to produce our estimate of total larval survivorship.

Natural mortality estimates were also taken from the literature (see Table 1). Those adults that survived had the additional possibilities of either growing to the next size class or staying in the same one. We used von Bertalanffy growth parameters (Ricker, 1975) to determine the chance that a fish of one size class grew to the next in a given year (Fig. 2). Von Bertalanffy parameters describe the growth of individual fish and are widely estimated in the literature (see Table 1 for the estimates that we used and

[1] Holland, D. S., J. B. Braden, and R. J. Brazee. 1995. Managing artisanal fisheries with marine fishery reserves: an alternative to managing catch or effort. Environmental and Natural Resources Policy and Training/Midwest Universities Consortium for International Activities Supplementary Paper 3, 36 p.

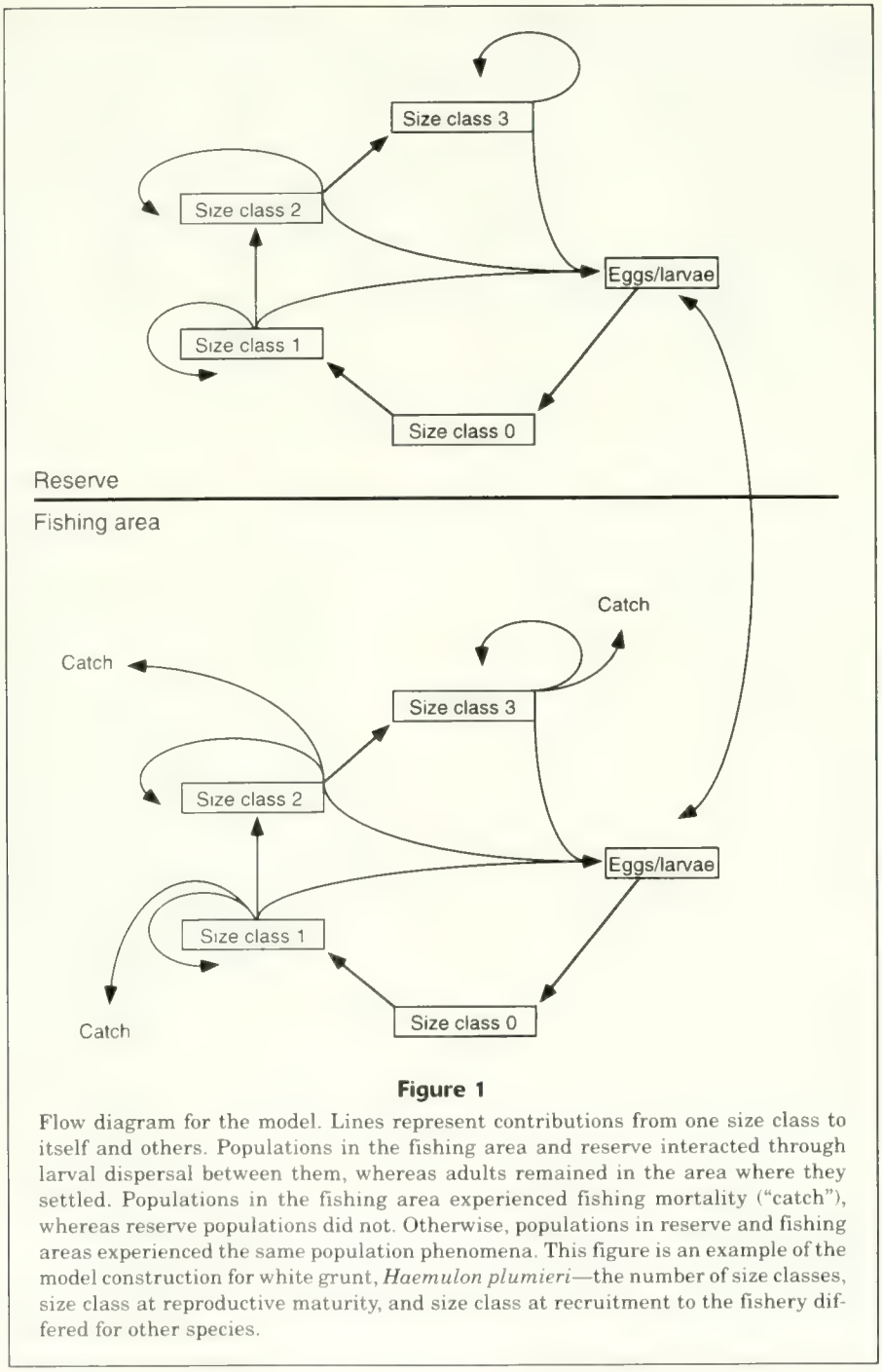

Figure 1

Flow diagram for the model. Lines represent contributions from one size class to itself and others. Populations in the fishing area and reserve interacted through larval dispersal between them, whereas adults remained in the area where they settled. Populations in the fishing area experienced fishing mortality ("catch"), whereas reserve populations did not. Otherwise, populations in reserve and fishing areas experienced the same population phenomena. This figure is an example of the model construction for white grunt, *Haemulon plumieri*—the number of size classes, size class at reproductive maturity, and size class at recruitment to the fishery differed for other species.

Appendix for relevant equations). To convert these continuous measures into probabilities, we used the standard von Bertalanffy parameters to estimate the lengths of the smallest and largest individual in each size category for the following year. We calculated the proportion of this size range that fell into the next size class and used this value to represent the probability that a fish of this size class grew to the next size class. The remaining individuals stayed the same size over the next year, with a probability determined by subtracting the probability of growing from 1. We chose the size-class interval for each species such that newly settled fish had exactly 100% chance of growing to the next size class during the first year (see Appendix for formula). Consequently, fish were never able to grow more than one size class in a year. As with all von Bertalanffy growth relationships, growth slowed with age—in our case from

Table 1

Parameter values for four fishery species. See Appendix for detailed explanation of parameters. Parameter values were taken from the literature where available. Where we could not find values in the literature, we made our best educated guess by looking at a related species, by running several values until we got realistic population growth (i.e. growth in the absence of fishing), or by measuring some other consequence, for example length at recruitment, to check for realism. References: (1) Plaut (1993); (2) Houde (1989); (3) Plaut and Fishelson (1991); (4) Aiken (1983); (5) Darcy (1983); (6) Thompson and Munro (1983); (7) best guess.

Species	Fecundity	Larval survival	Adult survival	Growth
Panulirus penicillatus, Red Sea spiny lobster	r = 4 spawns per year × 2.715 × $L^{2.581}$ eggs per spawn Mature at L = 50 mm (1)	D = 35.5 days (1) Z = 0.3454 (2) $N = 5 \cdot 10^{-6}$ (2)	v = 0.8 (M=0.223) Fishery recruitment = 25.7 mm (7)	k = 0.1066 L_∞ = 84.7 mm t_0 = 0 c = 6.43×10^{-4} y = 2.89 (3)
Balistes vetula, queen triggerfish	r = 3 spawns per year × 73 per g body weight Mature at size 23.5 cm (4)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \cdot 10^{-5}$ (2)	v = 0.07427 (M=2.6) (4) Fishery recruitment = 17 cm (7)	k = 0.57 (4) L_∞ = 45 cm (4) t_0 = –0.5 (7) c = 0.05164 (4) y = 2.875 (4)
Haemulon plumieri, white grunt	r = 1 spawn per year × (626 per g body weight – 93000) Mature at size = 22 cm (5)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \cdot 10^{-5}$ (2)	v = 0.17 (M=1.77) Fishery recruitment = 14.9 (5)	k = 0.34 (5) L_∞ = 42 (5) t_0 = –1 (7) c = 0.0238 (5) y = 2.93 (5)
Epinephelus guttatus the red hind	r = 1 spawn per year × 873.454 per g body weight – 194086) Mature at size < 25 cm (6)	D = 28.7 days (2) Z = 0.3454 (2) $N = 5 \cdot 10^{-5}$ (2)	v = 0.5066 (M=0.68) Fishery recruitment = 31 cm (6)	k = 0.24 (6) L_∞ = 52 (6) t_0 = –0.5 (7) c = 0.0107 (6) y = 2.96 (6)

100% growth for new settlers to 0% for fish in the largest size class.

Adults in the fishing area that grew larger than the minimum catch size experienced fishing mortality. We represented fishing mortality using the parameter u, equal to the proportion of fishery-recruited individuals caught per year, and related to the more common F by the equation:

$$u = 1 - e^{-F}.$$

We independently varied the two key parameters in our models: fishing mortality (u) and reserve proportion (s).

We made settlement a density-dependent process by incorporating a negative exponential function into survivorship for new settlers during their first year (see Appendix for equation). There is evidence to suggest that shelter is limiting for coral reef fish, especially new settlers (Hixon, 1991; Hixon and Beets, 1993; Hixon and Carr, 1997)—a process that would fit well with our density dependence assumptions. We also performed runs in which larval rather than new settler survivorship was density-dependent and

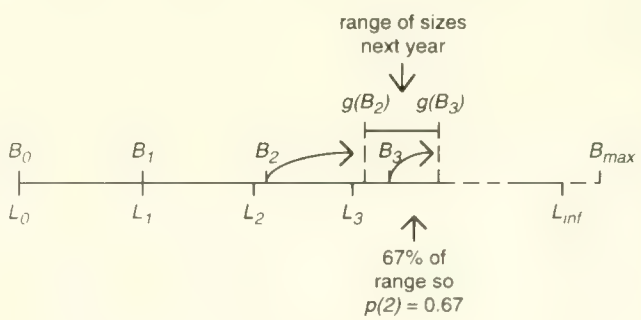

Figure 2

Determination of growth probabilities. The probability $p(x)$ that a fish of size class x grows to size class x+1 is the proportion of the range of sizes that size class x individuals will span one year later. Using von Bertalanffy growth parameters (see Appendix), we determined one year in the future the size of the smallest and largest fish in size class x. All other fish in x would fall between these two values. We then determined what proportion of these sizes fell into size class x+1, 0.67 in the case illustrated. In this hypothetical example, we would assume that $p(x)$ = 0.67, or that 67% of the fish from size class x grew to class x+1 by the next year. L_t represents the sizes attained at age t and B_x represents the lower bounds of each size class. We begin counting age at the moment of settlement (so $L_0 = B_0$).

obtained qualitatively identical results. Little information exists on density-dependent relationships for tropical fish; therefore we were forced to use a standard theoretical logistic equation (see Appendix). For simplicity in analysis and in recognition of this knowledge gap, we constructed the models with a fixed carrying capacity of 1000 one-year-old individuals per unit area. We modeled population processes on the basis of density measures in reserve and fishing areas and used relative proportions of each to calculate catches and population fecundity. Thus, yields are expressed as kg per year from the whole management area.

In order to ask the general questions we intended, we used two simple movement assumptions that emphasized the benefits accruing from larval transport rather than from adult spillover. Larvae dispersed widely across reserve boundaries, resulting in an even density of new fish settlement in reserve and nonreserve areas. This assumption does not negate the possibility that larvae drift to the open ocean and become lost—these can be accounted for in larval mortality. Rather, the assumption implies that settlement in the reserve and the management area are equally affected by the stock averaged over both areas. We also assumed that adults did not move across reserve boundaries; that is to say fish spent their entire lifetime in the area in which they settled. These assumptions specifically addressed the case where enhanced fecundity within the reserve was exported to fishing areas through larval transport. Thus they complemented previous models that focused on enhancements from adult spillover (Polacheck, 1990; DeMartini, 1993). These models also examined potential increases in reproductive output by means of increased spawning stock biomass per recruit. However, they were unable to examine the equilibrium consequences with their particular model construction.

Our movement assumptions apply to the majority of fishery species on at least some spatial scales. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996). Consequently, larvae are more likely to cross boundaries than are adults. As long as individual reserve units stretch beyond the dispersal distance of adults but remain well within the dispersal distance of larvae for a given species, the model assumptions will approximate reality. For large reserve proportions, our assumptions could still be met if the reserve area were partitioned into several smaller units. Some areas of concern here include ontogenetic and reproductive migrations. To fit the assumptions of this model, reserves must be designed with these movements in mind so that fish are likely to remain in the reserve during the phase of their life in which they are vulnerable to fishing.

We ran the models over reserve proportions varying from 0 to 99% of the management area (s=0 to 0.99), and fishing mortalities varying from 1% to 100% mortality of fishery-recruited individuals per year (u=0.01 to 1.00). For each combination of fishing mortality and reserve proportion, the model ran until the fish catch—calculated for the whole management area rather than per km^2 of available fishing area—had stabilized at the long-term sustainable yield. The model stored the yield, fishing mortality, and reserve proportion. It sometimes took hundreds of years to reach stability, and those interested in our model's predictions about the short-term dynamics of reserve creation should refer to Sladek Nowlis and Roberts (1997).

We used these results to determine the optimal reserve proportions and fishing mortalities for individual fishery species. For each fishing mortality, we found the reserve proportion that maximized sustainable yields and stored it and the yield. We compared these yields when an optimally-sized reserve was used with the yields without a reserve (s=0) to establish fisheries benefits. We plotted this information using fishing mortality as an independent variate.

We also examined the effects of marine fishery reserves on year-to-year catch variability. Bohnsack (1996) suggested that marine fishery reserves could dampen natural fluctuations in catches, thus making fisheries more stable and easier to manage. We tested this hypothesis by adding a stochastic component to larval survivorship in our model. These new models drew larval survivorship randomly from a normal distribution around the mean larval survivorship whose standard deviation we could define. We examined all species over a range of fishing mortalities and present the results from u = 0.2, 0.4, 0.6, and 0.8 to illustrate the pattern. We also examined some of these conditions at three levels of environmental variation, with standard deviations of 5, 10, and 20% of the mean larval survivorship, to gain insight into whether reserve benefits are influenced by the degree of environmental variability.

For each possible combination of fishing mortality and reserve proportion, we performed 10 replicate runs of our stochastic models. In each run, we ran the models for 500 years to allow the fisheries to stabilize to the maximum extent possible and thus minimize the influence of our arbitrarily chosen initial state. The mean and standard deviation of the catches were measured over the next 100 years. We examined the ratio of the standard deviation to the average catch over this period because this measure gave us an estimate of the likelihood of percentage fluctuations in catches rather than absolute changes.

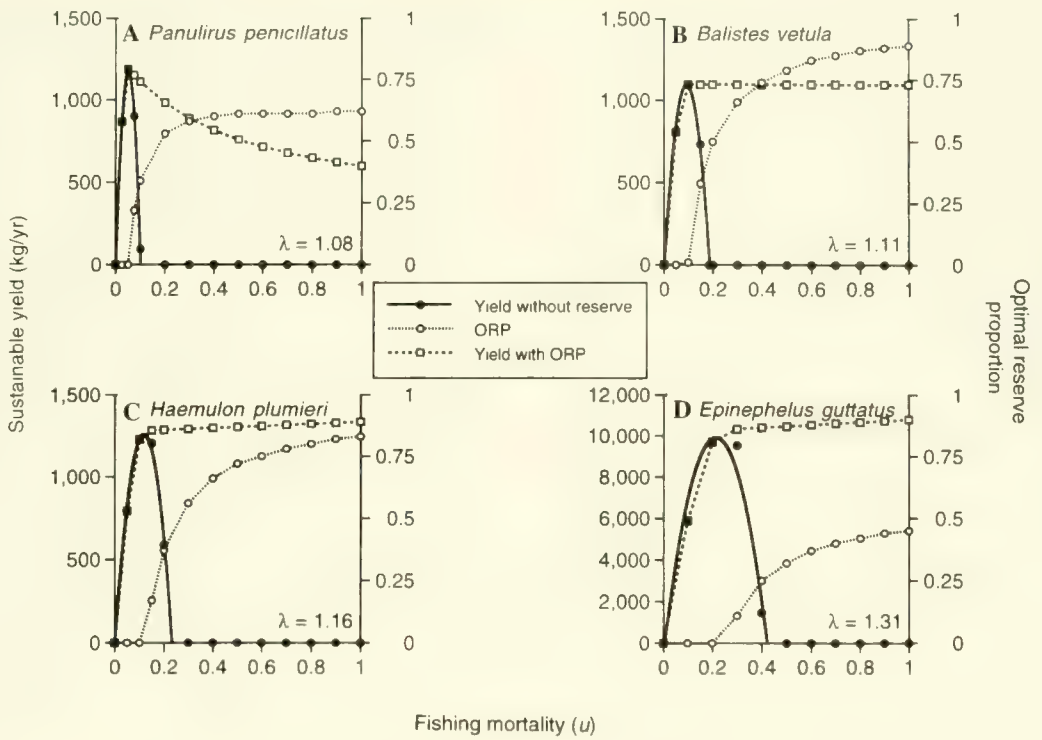

Figure 3

Optimal reserve proportions and corresponding yields. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. In all graphs, the solid circles and line represent the sustainable yield (kg of catch per year from the whole management area) that occurs in the absence of a reserve, the open circles and dotted line represent the optimal reserve proportion (that which produced maximum sustainable yields for each fishing mortality), and the dashed line and squares represent the sustainable yield when the optimal reserve proportion was used. Intrinsic population growth rates (λ) determine the robustness of the populations to fishing, high growth rates sustaining heavy fishing and low rates requiring reserves at low fishing mortalities.

This measure is better than standard deviation alone which would treat a 10-kg fluctuation equally, regardless of whether it occurred in a 100 kg or 1,000,000 kg per year fishery. We graphed these results with reserve proportion as the independent variate and examined the graphs for trends.

We performed these analyses on four coral reef fishery species for which we obtained relatively complete parameter sets. These included *Balistes vetula*, queen triggerfish; *Epinephelus guttatus*, red hind; *Haemulon plumieri*, white grunt; and *Panulirus penicillatus*, Red Sea spiny lobster (see Table 1 for parameter estimates).

Results

When we ran the models without a reserve (s=0), they produced standard yield-effort curves (Fig. 3). These curves are characterized by steep initial gains in long-term sustainable yields with increases in fishing mortality (and thus effort), followed by equally steep declines (Clark, 1990). The curves peaked at the maximum sustainable yield, one of several goals a manager might try to achieve with a fishery (Clark, 1990), and we will refer to the corresponding fishing mortality as the MSY mortality for the rest of this paper. Above the MSY mortality, the fishery can be defined as overfished because it is less productive than it would be with less fishing activity.

When a reserve was present, the yield-mortality curves were still parabolas passing through the origin but spread farther to the right, and the larger the reserve, the more pronounced were these shifts. Consequently, larger reserves required higher fishing mortalities to maximize long-term sustainable yields (remember that this mortality only affected fish in fishing areas), whereas the sustainable yields

decreased more slowly as fishing mortality increased past the MSY mortality.

Our analyses of optimal reserve proportions produced several key results. First, reserves produced fisheries enhancements, meaning that the overall catches with a reserve exceeded those without one, whenever the fisheries were overfished (Fig. 3), here defined as fished above the MSY mortality level. When fisheries were overfished, they produced higher yields with a reserve even though the reserve decreased the amount of fishing area. The optimal reserve proportion increased with increasing fishing mortality, and heavily exploited fisheries required particularly large reserves to remain productive. The fishery benefit attributable to reserves, calculated by subtracting the yield without a reserve from that with an optimally sized reserve, increased with increasing fishing mortality up to a near-maximum yield in most cases (Fig. 4). Consequently, a wide span of reserve sizes (up to 80% of the management area for some species) produced similarly high yields for most species as long as fishing mortalities were chosen accordingly.

Using this information (Fig. 3), we predicted optimal reserve proportions under real-life fishing mortalities. For queen triggerfish, the fishing mortality estimate of $u = 0.45$ from Puerto Rico and the Virgin Islands (Aiken, 1983) corresponded to an optimal reserve proportion of approximately $s = 0.8$. For white grunt, a reported heavy fishing mortality of $u = 0.99$ from Jamaica (Darcy, 1983) corresponded to an optimal reserve proportion of just over $s = 0.75$. Thus, for these species in these locations, our models predicted that 75–80% of the fishing grounds should be made off-limits to fishing in order to maximize long-term sustainable yields. These numbers may seem unrealistically high, especially since most models predict maximum yields when approximately 50% of the population density at carrying capacity is protected from fishing (see Clark, 1990, for an overview). In the case of our models, populations within the reserve did not reach carrying capacity when fishing was heavy outside, and the conditions of peak production corresponded to those that protected approximately 50% of the population density at carrying capacity.

The qualitative conclusions outlined above were consistent across all the species we examined. However, the model's quantitative predictions of the long-term fishery yields and optimal reserve proportion varied from species to species for any given fishing mortality (Fig. 3). The key differences between species were the speeds at which the yield and optimal reserve proportion changed with increasing fishing mortality (Fig. 3). These differences reflected differences in intrinsic population growth rates (λ)—the maximum growth rate of a population with no density-dependent constraints or fishing mortality. This summary parameter integrates most of the life history data that we used. It does not include the growth rate of individuals in the population and consequently does not adequately predict yields. However, it is a useful summary of the ability of a population to sustain harvesting. For example, life history parameters from the literature suggested that the Red Sea spiny lobster had a relatively low $\lambda = 1.08$, just above the $\lambda = 1$ necessary for a population to sustain itself with no fishing pressure. This species had a low MSY fishing mortality because its slow population growth could

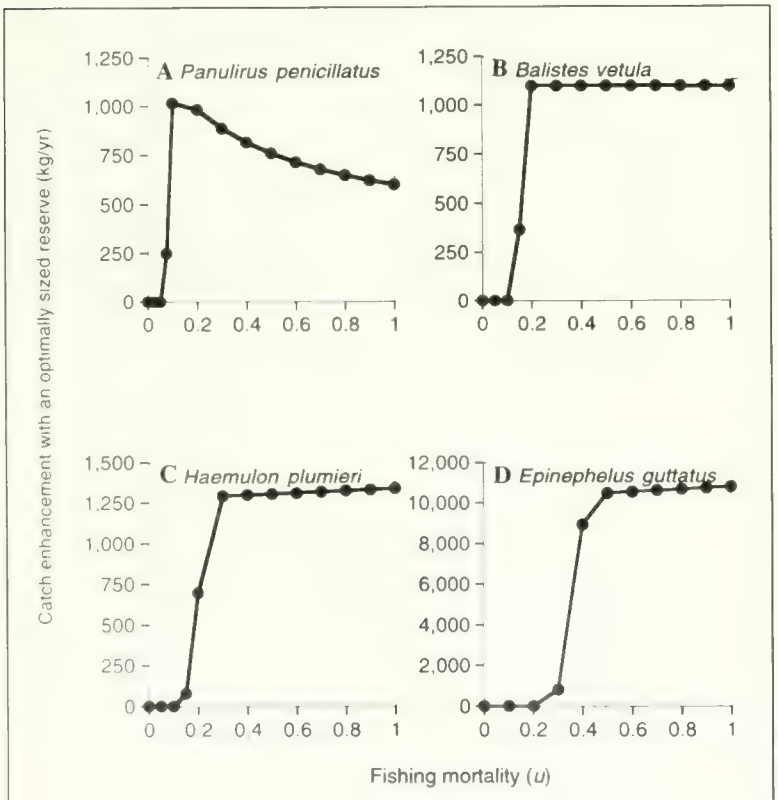

Figure 4

Catch enhancements with the use of an optimally proportioned reserve (OPR). (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Values represent the increase in yield, in kg of catch per year from the whole management area, one could expect if an optimally sized reserve system were established in a management area that lacked reserves initially.

only sustain modest harvesting effort (Fig. 3). In contrast, life history parameters from the literature suggested that red hind had a relatively high $\lambda = 1.31$. Consequently, its maximum sustainable yield occurred at the highest fishing mortality of any species we tested (Fig. 3). The two other species we examined had intermediate intrinsic rates of population growth rates and responses to reserves.

The sensitivity of our models' quantitative predictions was also clear within a species when we varied larval survivorship. For all species, optimal reserve proportion and yield without a reserve varied greatly (senior author's unpubl. data) because we varied larval survivorship from 10^{-5} to 10^{-4}. This sensitivity to poorly understood parameter values renders any quantitative estimates of optimal reserve proportion unreliable, whether the inaccuracy is in larval survivorship, the relationship, or parameters for density dependence, or any other life history parameter.

Finally, we examined how reserves might influence unpredictable catches resulting from environmental variation. Our stochastic models predicted that catches will be more stable with larger reserve proportions. In these models, we saw general decreases in catch variability with increasing reserve proportion (Fig. 5). The results presented here showed drops in variation that were more pronounced at higher fishing mortalities for all four species. We also tested these results at three levels of environmental variation. Our results showed that the drop in catch variability was most extreme when the environment was most variable, suggesting that the stability offered by reserves will be most valuable in highly variable fisheries.

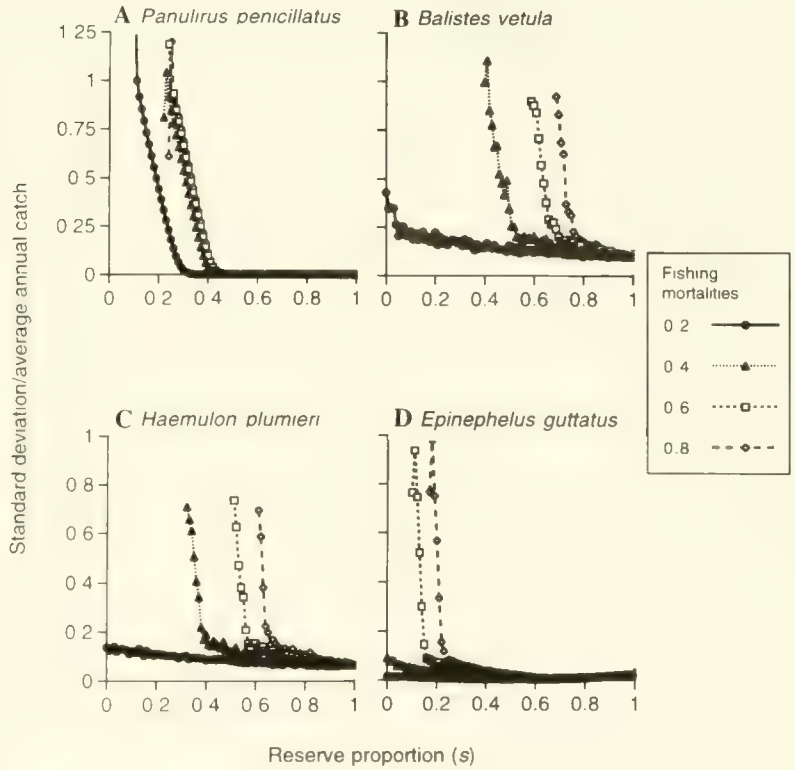

Figure 5

Catch variability and reserve size. (**A**) *Panulirus penicillatus*, Red Sea spiny lobster. (**B**) *Balistes vetula*, the queen triggerfish. (**C**) *Haemulon plumieri*, white grunt. (**D**) *Epinephelus guttatus*, red hind. Each graph shows decreasing catch variability with increasing reserve proportion at four levels of fishing mortality.

Discussion

Effects of life history and fishing mortality on reserve benefits

Our models predicted that marine fishery reserves will provide catch enhancements to any overfished fishery that meets our basic assumptions regarding the movement of adults and larvae. The results from previous modeling efforts by Man and colleagues (1995) and Holland and co-workers (Holland and Brazee, 1996; Holland et al.[1]) support these findings if one compares their results in specific cases to the patterns we found for a variety of species. Two key variables help determine whether a population is overfished: intrinsic population growth rate (λ) and fishing mortality. Managers can control fishing mortality to varying extents. Apparently, this control is inadequate in many industrial fisheries (FAO, 1995) and is probably even less effective in subsistence fisheries (Roberts and Polunin, 1993). Managers have no control over population growth potential but can take into account that species with low population growth have a greater tendency to be overfished and consequently show greater promise for fisheries enhancements from reserves.

Even in a well-managed fishery, it may be helpful to close large areas. This strategy could allow the relaxation of some fishing restrictions in remaining waters. Consequently, recreational and commercial

fishermen may feel greater equity with fewer restrictions on the number of participants or their catches. Moreover, reserves have the potential to reduce variability in catches from year to year and to enhance conservation of species and ecosystems. Fishing is not the only threat to marine ecosystems, though, and fisheries regulations are not sufficient to protect these systems (Allison et al., 1998).

To our knowledge, no field study has yet examined the effects of population growth potential or fishing mortality on reserve benefits. In part, such studies are made difficult by the uncontrolled nature in which reserves are established.

Relation of fishery benefits to reserve size

Real-world fisheries span a range from lightly fished to heavily overfished, and the optimal reserve size will depend on the fishing mortality as well as the population growth potential of the target species. Because many fisheries involve multiple species with widely divergent population growth potentials, choosing a single best reserve size may be difficult. Moreover, key aspects of the life history of marine fish, the larval phase in particular, remain a mystery. Because of these gaps in knowledge, it would be difficult to make an accurate prediction of the optimal reserve size even in a well-studied single-species fishery.

Although our research sheds doubt on the use of a universal reserve proportion, it does lend support for the use of large reserve systems under certain circumstances. In the two real-world cases where the necessary information existed, our models predicted that reserves should encompass 75–80% of the management area. These proportions are enormous and may be unrealistic for several reasons. First, the short-term economic losses from closing 80% of a management area would be large, although our models predict that the recovery time for such heavily overfished fisheries would be rapid (Sladek Nowlis and Roberts, 1997). Second, the political challenges of establishing such large reserves would be a formidable barrier. Finally, we do not stand firmly behind these predictions because their accuracy is dependent on parameter values that are poorly understood. Nevertheless, consistent results across several species suggest that reserves encompassing 40% or more of a heavily fished management area could produce substantial fisheries benefits.

Though rare, at least one large reserve system does exist. The Mombasa Marine National Park closed over 60% of local fishing grounds (McClanahan and Kaunda-Arara, 1996). This example fits nicely with our model's assumptions because levels of fishing effort remained similar in the fishing grounds before and after the closure. After two years, total yields had not surpassed those prior to reserve establishment (McClanahan and Kaunda-Arara, 1996). However, catch per unit of effort had increased dramatically and total yields showed potential for future increases. In this case and others involving extensive use of marine reserves, our research encourages an adaptive approach that reflects the lack of knowledge about fish life histories and the high degree of uncertainty in these complex biological systems.

Relation of reserve size to catch variability

Our model supported Bohnsack's (1996) hypothesis that catch variability will decrease with increasing reserve size. Our models predicted decreases in catch variability across a variety of levels of environmental variability and fishing mortalities. Our results also complement other studies that showed that reserves could reduce catch variability,[2] decrease the likelihood of bad years (Lauck et al., 1998), and increase the persistence of fisheries vulnerable to overfishing (senior author's unpubl. data).

To our knowledge, no field study has yet examined the effects of reserves on catch variability. Although they may be confounded by variability in fishing effort, the necessary data should be practical to collect before and after reserve creation.

Assumptions revisited

As with all models, one must be careful in interpreting the results of this one. It is based on parameter values that in some incidences—larval survivorship in particular—are poorly understood. However, the model's predictions are qualitatively robust to parameter errors, meaning that its general predictions hold true across a wide range of values and a wide variety of species. Our assumptions regarding the movement of adults and larvae were far more critical in influencing the conclusions we have drawn here.

Our assumptions regarding adult movement have wide applicability. Many fisheries target sessile organisms such as harvested kelp (Bustamente and Castilla, 1990), slow-moving organisms including many invertebrates (Davis and Dodrill, 1980; Davis and Dodrill, 1989), and organisms with high site-specificity such as many reef fish (Polunin and Roberts, 1996). All of these systems are likely to approximate our assumptions of no adult movement. This model is not universally applicable, as highly mobile and migratory species, including many pelagic fisher-

[2] Mangel, M 1998. Environmental Studies Board, University of California, Santa Cruz, CA 95064. Unpubl. data.

ies (Safina, 1993), will only fit our adult movement assumptions if large reserves are established. Recent studies, though, have shown high site fidelity by fish species previously thought to range widely (Holland et al., 1993; Holland et al., 1996), demonstrating the need for more field data on adult movement patterns. Moreover, recent modeling efforts by Holland and colleagues[1] and others[3] suggest that reserves can benefit highly mobile species through enhanced population fecundity gained from temporary protection.

If adults do cross reserve boundaries, our predictions regarding fisheries benefits from reserves will be influenced in opposing ways. Under heavy fishing pressure and intermediate movement tendencies, minor yield enhancements may be possible from this adult spillover (Polacheck, 1990; DeMartini, 1993). However, this same movement would dilute the ability of reserves to enhance larval transport to fishing areas. As Polacheck showed (1990), spawning stock biomass, or the potential for fisheries enhancement through larval transport, is highest at lowest levels of adult movement. Because the potential benefits from larval transport presented here far outweigh those predicted from adult spillover (Polacheck, 1990; DeMartini, 1993), it is likely that adult movement across boundaries will decrease the predicted yields from reserves. Consequently, reserves will have the highest potential for enhancing surrounding fisheries if they are designed as a collection of units large enough to contain populations of adults with relatively little movement across boundaries.

Our assumptions regarding larval transport have less supporting evidence. Most aquatic species disperse more widely as larvae than as adults (Boehlert, 1996), and the potential for long-distance dispersal across reserve boundaries is great for species with long-lived larvae (Roberts, 1997), including most food fish. Consequently, larvae are likely to move from reserves to fishing areas as long as oceanographic conditions and larval behavior permit. Without larval transport, the potential for fisheries benefits from reserves is more limited, although Holland and colleagues[1] did show that a reserve system in which larvae stayed in place but adults moved widely across boundaries could produce some benefits. Reserves, especially in heavily overfished or large management areas, may need to be partitioned into several subunits that maintain adult populations within them but allow larvae to disperse to remaining fishing areas.

We also assumed a stock-recruitment relationship, implying that a significant portion of the population fecundity from reserves stays in or returns to the management area. The degree to which marine populations are locally sustained remains an active area of debate in marine ecology. Larvae of most tropical food fish are often found in greatest quantities offshore (Boehlert, 1996), suggesting the possibility of long-distance dispersal. However, studies that show this result may be biased because sampling within the complex structure of the reef itself is difficult (Boehlert, 1996). Therefore, reefs may harbor greater concentrations of larvae than are measured above the reef. This complexity (Wolanski and Sarsenski, 1997), along with potential for larval behavior to influence their distribution (e.g. Breitburg et al., 1995), suggests that larvae may be retained at higher concentrations than predicted by simple oceanographic models (e.g. Roberts, 1997). If recruitment dynamics are influenced on a much larger spatial scale than encompassed by the management area, such that the stock in the management area has a minimal impact on recruitment back to it, reserve benefits to the management area are likely to be much more limited. Cohort models, including those by Polacheck (1990) and DeMartini (1993), can be interpreted as situations in which larval supply is constant and not influenced by local stock. As has been discussed, these models show limited potential for fisheries benefits from reserves. It is necessary to think of reserve systems at a scale that fits stock-recruitment relationships. Yet our knowledge of these relationships remains poor. Even if larvae have the potential to disperse over large distances, stock-recruitment relationships could still exist on a local level if a significant portion of larval production is retained. The safest approach to this uncertainty is to design reserve systems at large scales. However, there is still the potential for reserves to produce fisheries benefits on small scales if larvae have the capacity to be retained. Further research on stock-recruitment relationships in marine populations will be invaluable for resolving this pressing issue along with many others in fisheries management.

Field needs and testable predictions

Our results identify areas in need of additional field work and make testable predictions. The needs in regard to field work differ for our quantitative and qualitative predictions. The quantitative predictions were highly sensitive to all parameters that affected intrinsic population growth potential. The most important and least understood of these parameters is larval survivorship. We need significantly better information about the duration of the egg and larval stages of coral reef fishes and their daily mortality

[3] Guenette, S. 1998. Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada. Unpublished data.

risk. Until we understand these life history stages better, it will be impossible to make quantitatively accurate predictions of the optimal design of any fishery management strategy.

We also need better insight into how fecundity changes with size. Fecundity-size relationships should be fairly easy to measure and can be incorporated into any standard fishery study where adequate numbers of adults are sampled. We would further benefit from estimates of size-specific natural mortality. Few natural mortality estimates for coral reef fish species exist in the literature, and most that do are based on highly indirect methods of association. Marine fishery reserves actually offer the potential to generate more accurate predictions of natural mortality because fishing mortality does not confound the attempt in unfished areas. Moreover, despite numerous studies, we still have a poor understanding of population regulation and density dependence in coral reef fishes. This understanding is also necessary before we can generate accurate quantitative predictions of reserve benefits.

In contrast to the long list necessary to generate quantitative predictions, our qualitative predictions require additional knowledge in only one key area: fish movement. Because the qualitative predictions were robust across life history patterns, the key to knowing whether a fish species fits our assumptions is the movement of this species as eggs, larvae, and as adults. To some extent, we can skirt this issue because in our model, reserve size was based on proportion of coastline rather than actual size. Consequently, if we choose the management area to match the scale of fish movement, our model can fit most species. For example, a 20% reserve divided into areas of tens of hectares might ensure that adults of the species we examined here will stay in the area in which they settled while their larvae disperse widely among the reserve and nonreserve areas. In contrast, the management area might have to encompass whole ocean basins for the movement assumptions to fit bluefin tuna (Safina, 1993). Thus, we need to understand the movement dynamics of larvae and adults of a species to know the scales at which it will fit the assumptions of our model.

From the species that we ran and the resulting qualitative predictions of our model, we can generate a list of testable predictions. We predict that

1) Reserves will be beneficial for any over-fished population. Populations with low intrinsic growth rates and high fishing mortality stand to benefit the most, as is the case for the majority of reef fisheries in many regions of the world, such as the Caribbean. The location and size of the reserve will also affect reserve benefits. For a fair test of this prediction, reserve should be representative of typical fish habitat and large enough to contain a viable population of adults.
2) Although no universal best reserve proportion exists, we predict reserves will enhance fishery productivity even when they encompass areas much larger than those of current reserve systems.
3) Reserves will reduce variation in catches resulting from unpredictability in fishing mortality as well as recruitment strength and larval survivorship. Such an effect will simplify fishery management and increase the ability of fishermen to predict future income.

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Appendix

Fecundities

Fecundities were size-specific, but the general form of the equation relating size to fecundity varied from species to species. The specific relationships are listed in Table 1 as r. These r values were set to zero for all classes smaller than the size at maturity.

Larval survival

We used equations developed by Houde (1989) that relate ambient temperature during development to duration of larval stage, daily mortality risk, and probability of surviving through the entire larval stage.

$$D = 952.5\ T^{-1.0752} \quad (1)$$

$$Z = 0.0003149\ T \quad (2)$$

$$N = e^{-ZD}, \quad (3)$$

where T = ambient temperature during development, in degrees Celsius;
D = duration of larval stage, in days;
Z = probability of mortality, per day; and
N = probability of surviving through the entire larval stage.

Adult survival

We assumed that newly settled fish experienced density dependence. Thus, instead of surviving at a rate v_i like individuals in other size classes, their survival was weighted by a density-dependent function of the form $e^{-\rho/K}$ where ρ = the population density and K = a measure of carrying capacity arbitrarily set at 1000 due to a lack of information on carrying capacities for the fish we studied. Note that size-class-1 individuals included new recruits that survived and grew as well as old size-class-1 individuals that survived but did not grow to size class 2. Thus, at time t, the densities of size-class-1 individuals in the reserve ($S_{1,t}$) and the fishing area ($F_{1,t}$) are

$$S_{1,t} = v_0 p(0) S_{0,t-1} e^{-S_{1,t-1}/K} + v_1(1-p(1))S_{1,t-1} \quad (4)$$

$$F_{1,t} = v_0 p(0) F_{0,t-1} e^{-F_{1,t-1}/K} + v_1(1-p(1))F_{1,t-1}, \quad (5)$$

where v_x = the density-independent survival rate for individuals in size class x.

Note that the density in the fishing area is decreased later in the program to account for fishing mortality but only for size classes larger than the size at fishery recruitment. Also note that other size classes experience the density-independent survival rate v_x.

Growth

We began with standard von Bertalanffy equations (Ricker, 1975), relating length to age and weight to length (Fig. 2) and categorized them as described by Figure 2. Through algebraic manipulation, we established a formula for $g(B_x)$, the size of an individual projected one year in the future:

$$g(B_x) = e^{-k} B_x + (1 - e^{-k}) L_{inf}. \quad (6)$$

We used this formula to establish the following calculation for $p(x)$, the probability that an individual in size class x grows to size class x+1 by next year.

$$p(x) \quad \frac{g(B_{x+1}) - B_{x+1}}{g(B_{x+1}) \quad g(B_x)} = \frac{L_\infty \quad B_{x+1}}{L_\infty \quad st - L_0} = \frac{L_\infty - B_{x+1}}{L_\infty - L_1}. \quad (7)$$

Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*

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Abstract.—Snow crab (*Chionoecetes opilio*) and Tanner crab (*C. bairdi*) fisheries in the eastern Bering Sea are managed by using swept-area estimates of biomass based on an annual survey conducted with a 83-112 eastern bottom trawl. Estimates of net efficiency (i.e. the capture probability of crab that occur between the wing-tips of the trawl net) are needed to correct the biomass estimates for any size selectivity by the trawl. Data on net efficiency were obtained experimentally by attaching an auxiliary net beneath the trawl net to capture crab escaping under the trawl footrope. Net efficiency is then the quotient of the trawl catch divided by the combined catch of the trawl and auxiliary nets. Mathematical models of the relationship between net efficiency and carapace width were formulated and fitted to the experimental data. Net efficiency for both species first decreased with increasing carapace width until a minimum efficiency was reached near 50 mm carapace width. At larger sizes, efficiency increased asymptotically with carapace width. Net efficiency for mature female Tanner crab was lower (0.47) than for males and immature females combined (0.72) at the same mean carapace width as mature females (66–107 mm). Net efficiency did not differ between morphologically mature and immature male Tanner crabs of the same carapace width.

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The commercial fisheries for snow crab (*Chionoecetes opilio*) and Tanner crab (*C. bairdi*) in the eastern Bering Sea are managed by using swept-area estimates of biomass (Alverson and Pereyra, 1969) provided by an annual Alaska Fisheries Science Center (AFSC) bottom trawl survey. In addition to catch and swept-area data, such biomass estimates require a value for the sampling efficiency of the trawl[1] (i.e. the proportion of animals that are captured within the area spanned by the trawl doors; Dickson, 1993a). Trawl efficiency can be considered as a function of sweep efficiency (the proportion of animals within the path of the doors, bridles, and sweeps that are herded into the net path) and net efficiency (the proportion of animals that are captured within the path of the trawl net; Dickson, 1993a). For snow and Tanner crabs, owing to a lack of any contradictory evidence, sweep efficiency was assumed to be zero and net efficiency was assumed to be unity. The assumption of zero sweep efficiency has been subsequently supported by experiments on herding,[2] but the assumption of complete net efficiency has been contradicted by studies in which low-light video cameras have documented that even large male crabs could often escape under the footrope.[3] Such observations prompted us to experimentally estimate net efficiency of the 83-112 eastern trawl, the trawl used for the eastern Bering Sea surveys.

Previous studies of net efficiency, which were focused at various species of groundfish, indicated that efficiency generally increases with body size (Engås and Godø, 1989; Walsh, 1992). For snow and Tanner crab, however, biological attributes other than size could also influence efficiency. For example, mature males have longer legs and thicker chelae, in relation to their carapace width, than either mature females or immature males. Not only could the difference in body shape result in differing net efficiency, differ-

[1] Throughout this paper we will refer to the trawl as an entire fishing gear comprising the net, bridles, and doors.

[2] Somerton, D. A., and P. T. Munro. 1998. Estimating the sweep efficiency of a bottom trawl. Manuscript in preparation.

[3] Munro, P. T. 1998. Alaska Fisheries Science Center, 7600 Sand Point Way NE Seattle, WA. Unpubl. data.

ences in behavior between sexes or between mature and immature individuals but could also lead to differences in efficiency. Of particular concern is a possible difference in net efficiency between mature and immature males because such a difference could lead to a bias in the estimates of the carapace width at maturity and thereby affect commercial minimum width regulations.

We estimated net efficiency with an experimental approach pioneered by Engås and Godø (1989) that uses an auxiliary net attached beneath the trawl net to capture crab escaping under the footrope. If the auxiliary net spans the fishing width of the trawl net, from wing-tip to wing-tip, and captures everything passing beneath the footrope, then efficiency is estimated as the quotient of the trawl catch divided by the total catch of both the trawl and auxiliary net (Walsh, 1992; Dickson 1993b). The crux of such an experiment is then to design an auxiliary net with a footrope that exerts sufficient bottom contact to capture everything passing beneath the trawl footrope without causing enough added drag to alter the fishing efficiency of the trawl. Unlike the trawls examined in the studies of Engås and Godø(1989) and Walsh (1992), the 83-112 trawl lacks bobbins or rollers on the footrope and instead has a footrope consisting of a simple, rubber-wrapped cable. This difference in trawl design required several distinct differences in the design of the auxiliary net. In this paper we examine the application of this auxiliary net to estimate the efficiency of the 83-112 eastern trawl for snow and Tanner crabs.

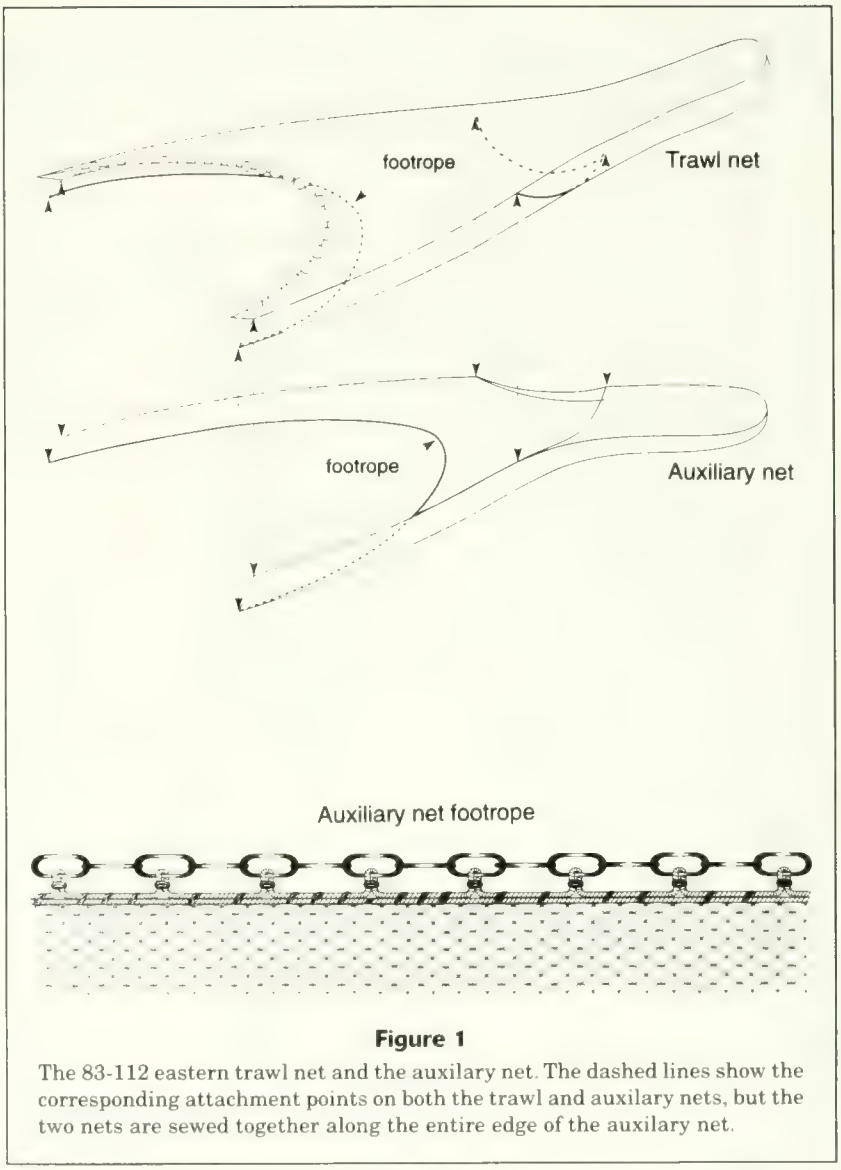

Figure 1

The 83-112 eastern trawl net and the auxilary net. The dashed lines show the corresponding attachment points on both the trawl and auxilary nets, but the two nets are sewed together along the entire edge of the auxilary net.

Materials and methods

Description of the trawl and auxiliary net

The 83-112 eastern trawl is a two-seam trawl with a 25.3-m headrope and a 34.1-m footrope consisting of a simple rubber-wrapped cable intended to remain in close contact with a smooth bottom (Fig. 1; see Armistead and Nichol, 1993, for a detailed net plan). The trawl is towed behind 1.8 × 2.7 m steel "V" doors weighing 816 kg each, which are connected to each wing with two 55-m bridles. Wing and throat sections of the net are made of 10.1-cm (stretched measure) nylon mesh, the intermediate section is made of 8.9-cm mesh and the codend is made with a double layer of 8.9-cm mesh lined with 3.1-cm mesh.

The auxiliary net was hung beneath the trawl net, attached at the wing tips and along the top of the wings (Fig. 1). Unlike the auxiliary net designs of Engås and Godø (1989) and Walsh (1992), our auxiliary net lacked a headrope, used the belly mesh of the trawl as the top panel, and had a single codend rather than three separate codends. The mesh used in the auxiliary net was the same as that for the trawl, but the footrope was longer (38.2 m) and was constructed of 16-mm long-link steel chain intended to be sufficiently heavy to excavate buried crab. An

additional feature of the auxiliary net was that the footrope was not attached anywhere along the length of the trawl footrope but instead joined it only at the wing tips. The auxiliary net footrope was intended to be positioned 2–3 m behind the trawl footrope along the center line of the trawl, but this position was not verified in the field.

Description of the experiment

The net efficiency experiment was conducted aboard a chartered 40-m stern trawler (FV *Arcturus*), from 20 July 1997 to 8 August 1997, immediately following completion of the annual AFSC trawl survey of the eastern Bering Sea. The experimental site was located east of the Pribilof Islands (57°11.4'N, 166°26.5'W) at depths between 75 and 90 m on a smooth bottom.

All hauls were made by using the same trawling procedure and towing speed (3 knots) as those used during the AFSC survey but tow duration (15 min) was only one half of the standard. Trawl net width, from wing-tip to wing-tip, was measured on all hauls with a SCANMAR net mensuration system.

The experiment began with test hauls of both the standard trawl and the trawl with the attached auxiliary net (experimental trawl) to determine if trawl performance was altered by the auxiliary net. All test hauls were conducted with the codends left open and with a video camera attached so that the trawl footrope near its center could be viewed. After three hauls of the experimental trawl, it became evident that the additional drag of the auxiliary net resulted in a reduction in the opening width of the trawl net. To help correct this problem, the bridles were shortened from the standard length of 55 m to 28 m. The shorter bridles were used for the remainder or the experiment.

All crab were removed from each catch and sorted into two groups: mature females, which were recognized by the presence of an enlarged abdomen, and all other crab. For simplicity, we will refer to the group "all other crab" as "mixed sexes." Carapace width, to the nearest 1 mm, was measured with vernier calipers on all individuals. On some hauls, randomly selected male Tanner crab were subsequently removed from the mixed sexes baskets and measured for both carapace width and chela height (right hand side) to allow determination of morphometric maturity.

Estimating net efficiency

Net efficiency (E_n) typically is an increasing function of body size (Engås and Godø, 1989; Walsh, 1992). To provide more flexibility, however, we modeled the relationship between net efficiency and carapace width as a function of two width-dependent processes: the probability of entering the net at the footrope (P_f) and the probability of entering the net through the belly mesh after escaping under the footrope (P_b). Algebraically this relationship can be expressed as

$$E_n = P_f + (1 - P_f)P_b. \quad (1)$$

The probability of entering the trawl at the footrope, was described with a three-parameter logistic function:

$$P_f = \frac{a}{1 + be^{-cw}}, \quad (2)$$

where a, b, and c = parameters; and
w = carapace width.

This function was chosen because it provides predicted values of P_f that increase with w asymptotically to a value of a and permits cases where efficiency is less than unity even at the largest body sizes. The probability of entering the trawl through the belly mesh was described by a two-parameter decreasing logistic function:

$$P_b = 1 - \frac{1}{1 + de^{-fw}}, \quad (3)$$

where d and f = parameters.

This function was chosen because it provides predicted values of P_b that decrease with w asymptotically to a value of zero.

The model resulting from substituting Equations 2 and 3 into Equation 1 was fitted to values of net efficiency for each 1-mm increment of carapace width by using a maximum likelihood procedure where the number of crab captured in the trawl net at each carapace width was described by a binomial random variable (Millar, 1992). The parameters of the model were estimated by minimizing the negative logarithm of the likelihood function:

$$L = -\sum_w \left(n_w \log E_{n,w} + (N_w - n_w) \log(1 - E_{n,w}) \right), \quad (4)$$

where, at each value of carapace width w,

n_w = the number of crab captured in the trawl net;
N_w = the total number of crab in the trawl and auxiliary nets combined; and
$E_{n,w}$ = the net efficiency.

N_w and n_w were calculated by pooling together the data from all good tows. For mature female crab, a simplified model consisting of only the P_f term was fitted to data because the smallest mature females were too large to fit through the belly meshes of the trawl net. In both cases, the models were fitted to the data by using the S+ function MS (Venables and Ripley, 1994).

The 95% confidence intervals for $E_{n,w}$ were estimated by using a bootstrap analysis (Efron and Tibshirani, 1993) which considered between-haul variability but ignored within-haul binomial variability which is relatively small. Each bootstrap estimate of $E_{n,w}$ was calculated by randomly sampling individual hauls with replacement from the original data, then by fitting the model to the data from the chosen hauls pooled together. After replicating the bootstrap process 240 times, values of $E_{n,w}$ at each increment of carapace width were then ranked. The upper and lower confidence intervals were chosen as the values of $E_{n,w}$ ranked 7^{th} and 234^{th} at each width increment.

Two tests of model form were conducted. First, to determine if the P_b term was a significant contribution to the model, the goodness of fit of the model, including both the P_f and P_b terms (five parameters), was compared to that of a model including only the P_f term (three parameters) by using a likelihood ratio test (pages 153–155 in Hilborn and Mangel, 1997). Second, to determine if the models for mixed sexes differed between crab species, the summed likelihoods of the model fit to each species were compared with the likelihood from a model fitted to the combined data for both species by using a likelihood ratio test. For both tests, significance of the likelihood ratio was evaluated by using a chi square statistic with degrees of freedom equal to the difference in parameters between the models being tested (Hilborn and Mangel, 1997).

In addition to the tests on model form, two tests were also conducted for differences in net efficiency between biological subgroups of Tanner crab. First, a test was conducted to determine whether net efficiency differs between mature females and mixed sexes restricted to the same range of carapace width as mature females. Because of the restricted range of carapace widths, we assumed that net efficiency could be modeled as a simple logistic function of carapace width and sex. This model was fitted by using the S+ function GLM (Venables and Ripley, 1994). Second, a test was conducted to determine whether net efficiency for mature male Tanner crab differed from that for immature male Tanner crab of equal size. Male crab were categorized as either immature or mature on the basis of height of their chela in relation to their carapace width by using the computer technique of Somerton (1980). Both categories were then restricted to a common range of carapace width that was spanned by the smallest mature and the largest immature individuals. Net efficiency was then modeled as a function of maturity and carapace width by using logistic regression. Significance of the sex term in the first test and the maturity term in the second test were assessed with analysis of deviance (page 186 in Venables and Ripley, 1994). When a term was significant, the resulting model was evaluated to predict net efficiency for each biological class at the midpoint of the carapace width interval examined.

Results

Effect of the auxiliary net on trawl performance

The attachment of the auxiliary net to the trawl net resulted in a decrease in wing spread, presumably from increased drag on the bottom. During the testing phase when the codends of both the trawl and auxiliary nets remained open, average wing spread for hauls with standard 55-m bridles was 14.3 m (n=3), considerably less than the mean width of the standard net (mean=17.0, n=29) used during the preceding survey hauls with the same length of towing cable. To help compensate for the additional drag of the auxiliary net, we shortened the bridles to 28 m. This increased average wing spread to 15.4 m (n=4). When the codends were closed, however, the auxiliary net rapidly filled with epibenthic fauna, especially brittlestars, resulting in a progressive narrowing of the wing spread by as much as 3 m over the duration of a haul. After seven attempts at trawling in the initial study area, we were forced to locate a new study area with a lower abundance of brittlestars. The progressive narrowing was nearly eliminated by the change of sampling site, but the mean wing spread during the remainder of the experimental hauls (mean=15.9, n=24) was still significantly less (t-test, t=5.18, P<0.001) than the standard net.

Although the wing spread was less during the experiment than during the AFSC survey, the departure from the standard width may not have been great enough to affect footrope contact with the bottom. Footrope contact at the center of the trawl was evaluated by using a video camera for three tows of the standard trawl (mean width=17.5 m), three tows of the experimental trawl with standard bridles (mean width=14.3 m), and three tows of the experimental trawl with short bridles (mean width=15.3 m). In all cases, the footrope in the bosom of the trawl did not contact the bottom, as evidenced by the lack of mud clouds behind the footrope, but instead

skimmed over the bottom at an estimated height of 1–2 cm. No difference in the proximity of the footrope to the bottom could be visually detected among the three trawl configurations. Because the range in wing spread among the three configurations was greater than the difference between the survey average and the experiment average, it is likely that the addition of the auxiliary net did not alter the contact of the footrope in the center of the trawl where most of the escapement usually occurs (Walsh, 1992).

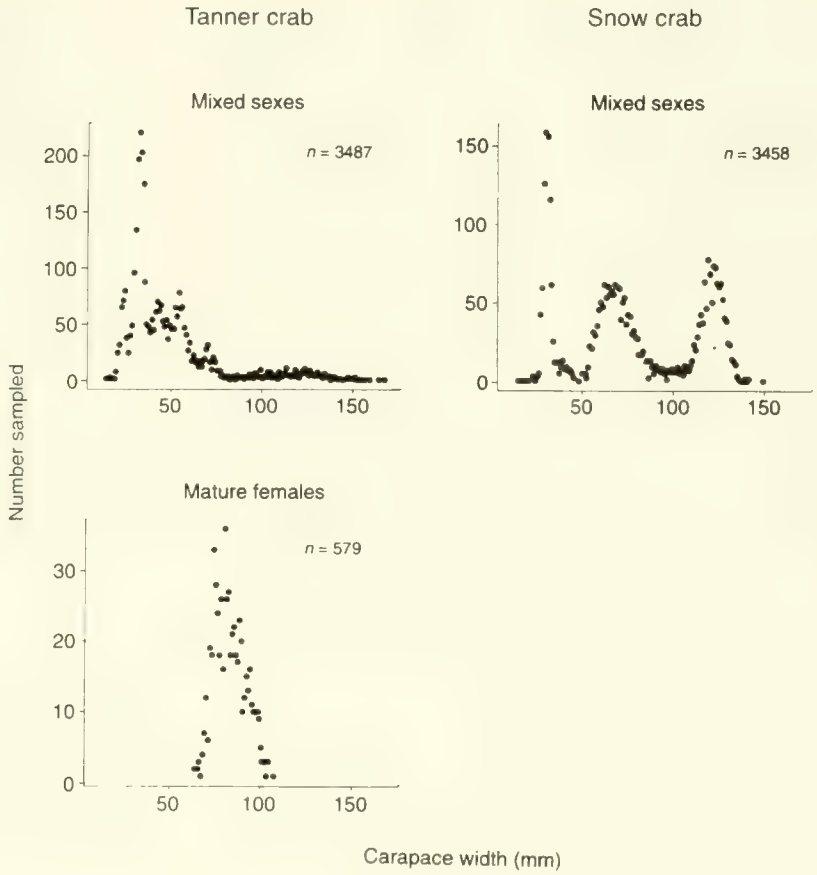

Figure 2

Carapace-width frequency distributions for the mixed sexes of snow crab (*Chionoecetes opilio*) and for the mixed sexes and mature females of Tanner crab (*C. bairdi*)

Description of the data

Thirty-one hauls of the experimental trawl were completed, but the data from the first seven were not used in subsequent analysis because of unusual trawl performance (the narrowing of wing spread associated with large catches of epibenthic fauna in the auxiliary net). For snow crab, width measurements were collected from 3458 individuals from the mixed sexes category, but from only three individuals from the mature female category. The low sample size for mature females prevented further analysis. Carapace-width frequency distributions indicated that a broad range of carapace widths was sampled, but the observations were concentrated in three carapace width modes (Fig. 2). For Tanner crab, width measurements were collected from 3487 individuals from the mixed sexes category, and from 579 individuals from the mature female category. Sampling for both categories covered a broad range of carapace widths, but for the mixed sexes category the observations were concentrated at smaller carapace widths. Plots of net efficiency against carapace width (Fig. 3) for the mixed sexes groups of both species showed an initial decline with increasing width until a minimum in net efficiency was reached in the range of 40–50 mm, then a steady increase as carapace width increased. For mature female Tanner crab, the narrow range of carapace widths and the large variance in net efficiency obscured any obvious change in net efficiency with carapace width (Fig. 3).

The fitted models

For the mixed-sexes category of both species, the models that included both the P_f and P_b terms fitted the data significantly better than the models with only the P_f term (Tanner crab, likelihood ratio=189.7, $P<0.001$; snow crab, likelihood ratio=60.5, $P<0.001$). This indicates that the apparent increase in net efficiency at small sizes is statistically detectable. Likewise, the separate-species model fitted the net efficiency data significantly better than did the combined species model (likelihood ratio=85.5, $P<0.001$). This indicates that the change in net efficiency with width differs between species. Plots of the fitted models (Fig. 3) indicated that the predicted values of P_b decline rapidly with increasing carapace width and become negligible at about 50 mm for Tanner crab and 60 mm for snow crab. For mature female Tanner crab, the model considering only the P_f term fitted the data significantly better than did the sample mean (likeli-

hood ratio=4.27, P=0.014), indicating that net efficiency increased significantly over the narrow width range of mature females (66–107 mm). Estimated parameter values for the fitted models are shown in Table 1.

For male Tanner crab, net efficiency for mature males (0.82, n=99) was not significantly different (analysis of deviance, P=0.47) than for immature males (0.81, n=39) at the center of the width interval spanned by the largest immature and the smallest mature individuals. This indicates that mature males are not preferentially selected by the survey trawl. For mature female Tanner crab, net efficiency (0.47, n=578) was significantly different (analysis of deviance, P<0.001) than the value for the mixed-sex group (0.72, n=441) at the midpoint of the mature female size range. This finding indicates that net efficiency was substantially less for mature females than for the mixed-sexes category (combined sexes excluding mature females).

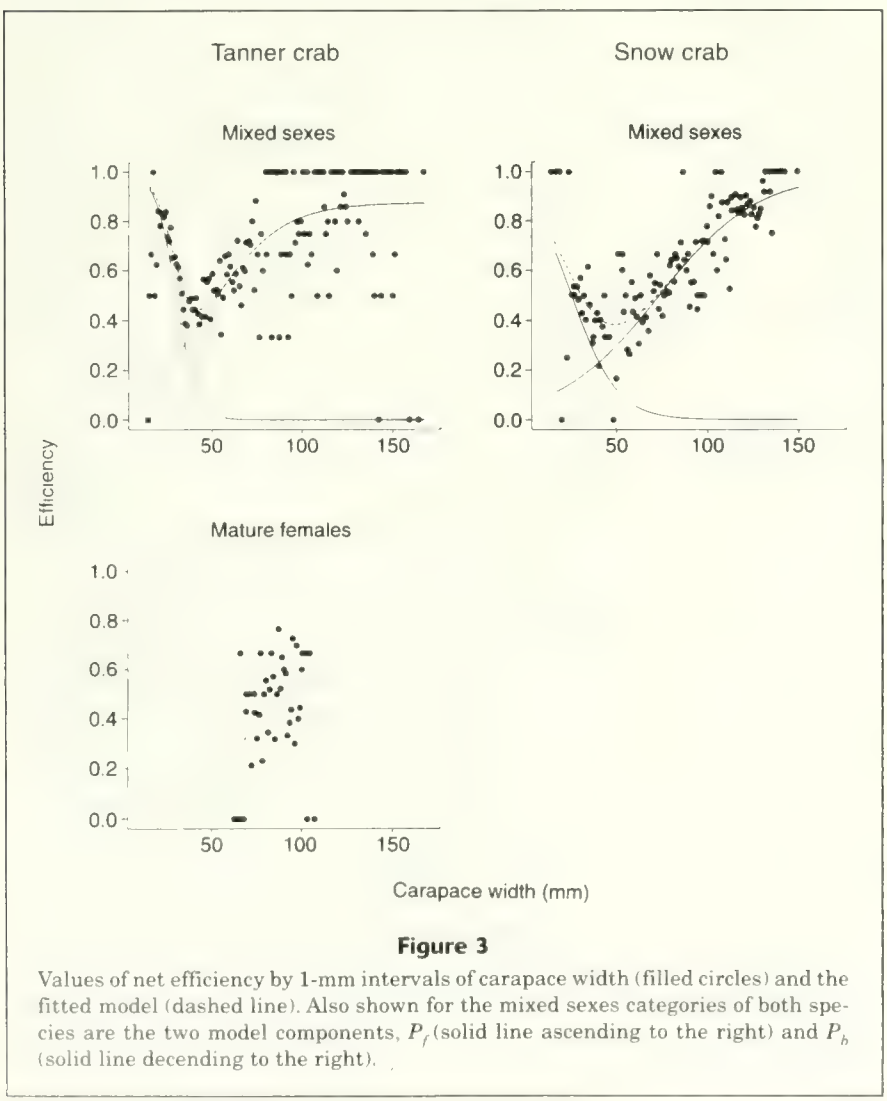

Figure 3

Values of net efficiency by 1-mm intervals of carapace width (filled circles) and the fitted model (dashed line). Also shown for the mixed sexes categories of both species are the two model components, P_f (solid line ascending to the right) and P_b (solid line decending to the right).

Discussion

Experimental trawl performance

Net efficiency estimates from auxiliary net experiments are potentially subject to two sources of bias. First, bias may result if the efficiency of the experimental trawl differs from that of the standard trawl. Of particular concern is any distortion of trawl geometry caused by the auxiliary net that changes the position of the footrope and fishing line in relation to the bottom. In our case, trawl net width was reduced by the increased drag of the auxiliary net. We attempted to compensate for this increased drag by reducing the bridles to one half of their standard length, but the resulting trawl net width was still approximately one meter less than the standard. The decreased trawl net width, however, apparently did not alter the proximity of the footrope to the bottom because our video observations did not reveal any conspicuous differences between the standard and experimental trawls. Although these observations were confined to the center of the footrope, previous video observations of the 83-112 trawl indicated that the center of the footrope tends to have lighter bottom contact than the wings and is therefore the area most likely to be impacted by the auxiliary net.

Second, bias may result if the experimental trawl cannot sample all habitats sampled by the standard trawl. To be effective, the footrope of an auxiliary net must fish harder on the bottom than the footrope of a trawl net. Consequently, the auxiliary net is more prone to damage from snagging on rocks and from filling with epibenthos and debris. Although, in our case, the chain footrope on the auxiliary net may have been effective at excavating buried crab, it also resulted in large catches of epibenthic fauna which, in turn, aggravated the problem of narrowed trawl width. We reduced the narrowing by moving the experiment to a location lacking high quantities of epibenthos, but by doing so we

Table 1

Parameter estimates of the fitted models for the mixed sexes of snow crab (*Chionoecetes opilio*) and the mixed sexes and mature female categories of Tanner crab (*C. bairdi*).

Parameter estimates	Snow crab mixed sexes	Tanner crab mixed sexes	Tanner crab mature females
a	0.9894	0.8743	0.5500
b	14.49	10.95	2003.0
c	0.0366	0.0504	0.116
d	7.905	185.9	
f	0.0810	0.1742	

excluded from consideration a type of habitat occupied by snow and Tanner crabs. Thus the net efficiency estimates we obtained may not be representative of the entire area covered by the survey.

Model form

The form of the model that we chose to describe the relation between net efficiency and carapace width included a term (P_f) that increases with width to account for entry into the trawl over the footrope and another term (P_b) that decreases with width to account for entry of crabs through the belly meshes of the trawl after they have passed under the footrope. The model with both P_f and P_b terms fitted the mixed-sexes data of both species significantly better than the model with only a P_f term, confirming the significance of the apparent increase in net efficiency with decreasing size at carapace widths less than 50 mm. However, we have been unable to verify that the increased efficiency is indeed due to the entry of small crab through the belly meshes. Regardless of the mechanism, the important question is whether the increase in net efficiency at small size is a normal property of the 83-112 trawl or an artifact of the experiment. We attempted to answer this question by comparing the width distributions of crab captured in the trawl net of the experimental trawl with those captured in the standard trawl at the same or nearby stations during the survey preceding the experiment, but patchiness and small sample sizes made the results equivocal.

In light of this uncertainty, the composite form of the model is advantageous because it allows separation of the P_f and P_b effects. For example, if further research reveals that the increase in efficiency at small size is associated with the attachment of the auxiliary trawl, then an estimate of net efficiency without this effect can be obtained by deleting the P_b term and by evaluating the reduced model with the parameters from the fit of the complete model (Table 1). For this reason, the bootstrapped confidence intervals we provide (Fig. 4) are computed two ways, by evaluating the full model and by fitting the full model but evaluating only the P_f term. However, because the P_b term decreases rapidly with carapace width, the full and reduced models predict nearly identical values of net efficiency at carapace widths above 50–60 mm, which includes the mature and commercial width ranges for both species.

Efficiency differences between biological subgroups

The survey trawl is less efficient for mature female Tanner crab than for the mixed-sexes group over the same range of carapace width. Since the mixed-sexes group is primarily male at these sizes, the difference in efficiency is likely due to between sex differences in both morphological features and behavior. Male Tanner crab have longer legs, in relation to their carapace width, than do mature females. Not only does this increase their effective size in relation to the trawl mesh but also may result in their bodies being held higher off the bottom in relation to the footrope. In addition, male Tanner crab may be caught more efficiently because they are less sedentary than females and less prone to bury themselves.[4]

The survey trawl efficiency does not differ between mature and immature male Tanner crab. We were concerned that mature males, which have larger claws and are perhaps more active than immature males, might be preferentially selected. If such selection did occur, it would lead to an underestimate of the carapace width at maturity which is used in establishing minimum width limits for the commercial fishery. Apparently such preferential selection of mature males does not occur.

In the foregoing, we estimated values of net efficiency or the capture probability of crab that occur between the wing-tips of the trawl net. For stock assessment purposes, however, it may be more convenient to consider these values expressed as trawl efficiency or the capture probability of crab that occur between the trawl doors. In situations where the bridles herd animals into the path of the trawl, further experiments to estimate sweep efficiency would be required to estimate trawl efficiency (Dickson, 1993a, 1993b). However, experiments on herding snow crab indicate that this species is not herded by the bridles of the 83-112 eastern trawl.[2] Thus, trawl efficiency can be estimated simply by multiplying net efficiency by the quotient of the net width divided by the door width (i.e. 0.30).[2]

[4] Stevens, B. 1998. Kodiak Laboratory, National Marine Fisheries, P.O. Box 1638, Kodiak, AK. Personnal commun.

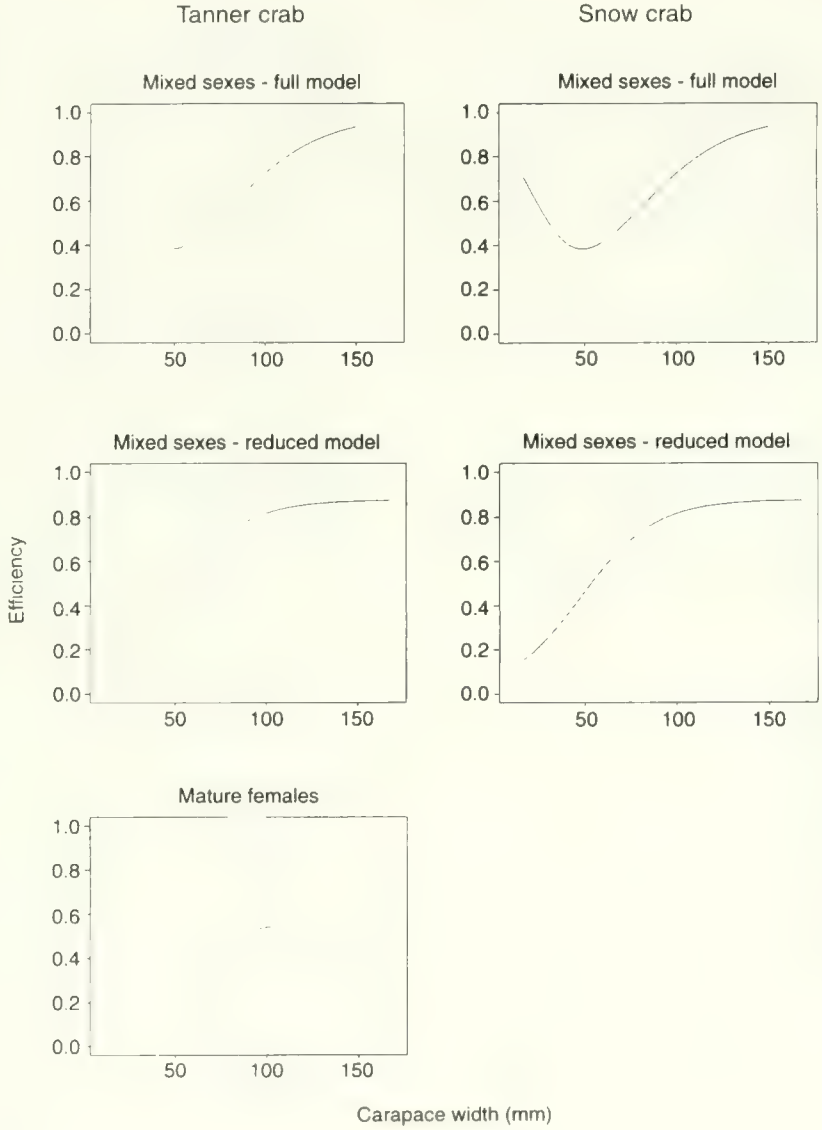

Figure 4

Fitted model and 95% bootstrap confidence intervals about the predicted value of net efficiency. For the mixed-sexes categories of both crab species, values of net efficiency are predicted in two distinct ways after fitting the full model (Equation 1) to the data. First, net efficiency was predicted by evaluating both P_f and P_b terms of the model (top row), based on the assumption that the entry of small crabs into the trawl net through the belly mesh occurs during normal trawl operations. Second, net efficiency was predicted by evaluating only the P_f term (i.e. setting P_b=0), based on the assumption that the entry of small crab through the belly mesh was an expermental artifact caused by adding the auxiliary trawl (second row).

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Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico*

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Abstract.—We sampled inner shelf habitat in the northeast Gulf of Mexico, for age-0 red snapper, *Lutjanus campechanus*, to estimate growth rates and seasonality, as well as to identify nursery habitats. We collected 7507 age-0 red snapper in 1994 and 1995, from 536 10-min trawl tows. Red snapper first settled to benthic habitat in June after reaching 17.4 mm standard length (age=26 d). In both years, catch per unit of effort (CPUE=number/10-min tow) peaked July through September, then declined in the fall as fish were leaving the habitat before winter. Most fish (80–81%) were caught at one location, 13 km south of Mobile Bay, Alabama. At this location in 1995, the August CPUE ±SE (712 ±243) far exceeded all previous estimates. Based on otolith microincrements, hatching-date frequencies showed distinct cohorts in June and July 1994 and May and June 1995. Growth rates for the June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994 were significantly faster compared with growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995. Density-dependent mechanisms may be operating with faster growth rates and lower CPUEs in 1994, compared with slower growth rates and higher CPUEs in 1995. However, environmental constraints may also be operating, as indicated by the slow growth rate of the May 1995 cohort that probably resulted from colder temperatures. Newly settled red snapper were aggregated on the inner shelf, at a particular location and time period. These concentrations indicated an important nursery habitat just south of Mobile Bay, Alabama, from July through September.

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To enhance survival some fishes spawn many times within a given season (Lambert and Ware, 1984). This strategy may produce several distinct cohorts at the juvenile stage within that season (Szedlmayer et al., 1990), and individual cohorts may have an advantage over others owing to biotic and abiotic environmental factors (Miranda and Hubbard, 1994). For example, faster growth may increase survival because fish grow past size-specific predators more quickly than slower growing fish (Houde, 1987; Sogard, 1997).

Red snapper, *Lutjanus campechanus*, have an extended spawning season (Moseley, 1966; Collins et al., 1996) and within-year variations in early life stages might be expected, but information on the age-0 juvenile stage of red snapper is sparse, especially at first settlement. Baughman (1943) suggested that immature fish came close to shore, but this observation was based on only five juvenile red snapper. Ogren and Brusher (1977) indicated inshore nursery areas for age-0 red snapper in the deeper portions of St. Andrew's Bay, Florida, but catch rates were low—a total of 62 fish in 312 10-min trawl tows. Bradley and Bryan (1975) caught young red snapper during summer months and suggested that juvenile red snapper sought deeper water as they grew older, albeit their catch rates were also low, with a maximum of 10 fish/10-min tow. Holt and Arnold (1982) showed a bimodal size distribution in juvenile red snapper from June through December, but this pattern was derived from separate year classes, where red snapper reached 110–130 mm during their first year, 220–230 mm during their second year. Age-0 red snapper were conspicuously absent from that study in July, and only 26 age-0 red snapper were collected in three years of August samples. Szedlmayer and Shipp (1994) reported a catch rate for age-0 red snapper in July 1991 that exceeded all previous studies (130 fish/10-min tow), but their effort was low with only 17 trawl tows in July, August, and October.

Despite these previous efforts, no study has specifically targeted age-0 red snapper just after settlement. Thus, we suspected that the primary nursery habitats used by first settlers had not been adequately sampled. In the present study we examine the early life stage of red snapper just after settlement. We determine growth rates, distribution, seasonality, and

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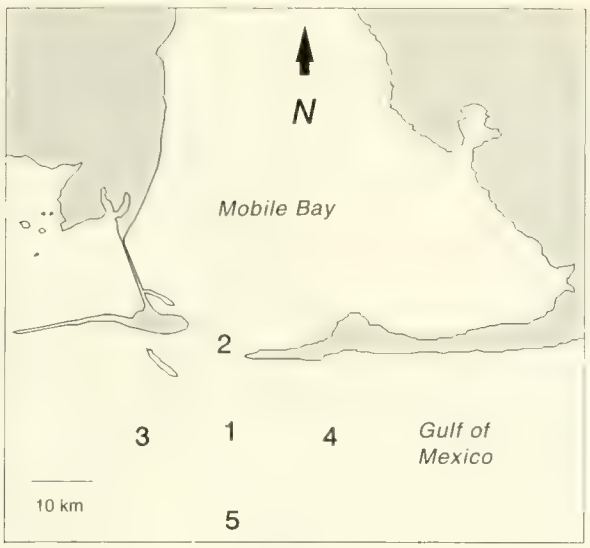

Figure 1
Map of station locations in the northeast Gulf of Mexico.

abundance; and identify multiple cohorts and primary nursery areas for this species.

Materials and methods

Age-0 red snapper were collected 0–26 km south of Mobile Bay, Alabama. Fish were sampled by trawl (7.62-m head rope, 2.54-cm mesh, 2-mm codend mesh). Five 10-min tows were taken every two weeks, at five fixed stations, from June 1994 through January 1995, and from June 1995 through January 1996 (Fig. 1). Sampling periods were sometimes longer owing to poor weather.

All trawl tows were made with a 6:1 ratio of towing cable length to depth, and tow speeds of 40 to 80 m/min. Bottom dissolved oxygen, salinity, and temperature were recorded with a Hydrolab Surveyor II. We did not sample in May but were able to plot temperature data measured at 1 m depth, for May through December, from a NOAA buoy moored 70 km west of the sites. Sediment samples were collected by SCUBA divers and examined by grain size analysis (Holme and McIntyre, 1971).

All age-0 red snapper were stored on ice in the field and later frozen in the laboratory. Fish were thawed, weighed to the nearest 0.01 g with an Ohaus balance, and measured with a caliper to the nearest 0.1 mm standard length (SL).

Sagittal otoliths were removed from all age-0 red snapper and mounted in epoxy (Spurr, 1969). Left and right sagittal otoliths were assumed to be identical; only one otolith was used to estimate age from a particular fish. Otoliths mounted in epoxy were first cut with a Buehler diamond blade saw, then mounted on glass slides with Crystalbond thermoplastic cement, and ground on both sides in the transverse plane to the primordium, on 400 and 600 grit wet-dry sand paper. Type A alumina powder (0.3 µm) and Buehler polishing cloth were used for final otolith preparations (Secor et al., 1991).

Microincrements of otoliths were counted from the primordium to the margin, along the sulcus ridge, in the transverse plane. We made all counts at 750× magnification, using a Sony GVM video monitor, a Sony CCD video camera, and an Olympus BH2 light microscope.

Two independent blind counts were made on each otolith. If the two independent counts were within 10% of each other, their mean value was used to estimate age. If the two counts differed by >10%, a third blind count was made. The means of the two closest counts were then used to estimate ages. If counts still differed by >10 % after three counts, the otolith was rejected.

Age of each fish was subtracted from date of capture for hatching-date estimations. Hatching-date histograms were plotted after applying a three-day moving average for each year, and local minima were used to separate cohorts (Szedlmayer et al., 1991). A significance level of ≤ 0.05 was used for all statistical analysis. Catch per unit of effort (CPUE=mean number/10-min tow) was estimated for each sample date and station. Prior to analysis CPUEs were $\log(x+1)$ base-10 transformed. Two-way analysis of variance (ANOVA) was used to test for significant differences in mean CPUEs and mean SLs among dates and stations. Waller-Duncan's multiple comparison test was used to show specific differences detected by the ANOVAs.

Growth rates were estimated by linear regression of SL on collection date, and SL on age from otolith microincrement counts. Analysis of covariance (ANCOVA), Student's *t*-test, and Tukey's multiple comparison test were used to compare estimated growth rates (Zar, 1984).

Results

Salinity ranged from 30.5 to 35.4 ppt, dissolved oxygen from 3.7 to 7.9 ppm in 1994. Temperature increased from 22°C in June to a peak of 29°C in August, then decreased to 17°C by January 1995. The temperature (26°C) in early June 1995 was higher compared with the previous year, stayed near this level through July, increased to 30°C in September, then decreased in the fall (Fig. 2). Temperature data from the NOAA buoy indicated that temperatures

were probably colder in May of both years at the sample sites (Fig. 2). Temperature, salinity, and dissolved oxygen were similar among stations (Table 1). Visual observations of debris in trawl samples indicated shell deposits at station 1 that were not apparent at other stations. Grain size analysis indicated similar sediments between stations 1 and 5, and between stations 2 and 4, whereas station 3 had a significantly higher silt-clay fraction compared with all other stations (ANOVA, $P \leq 0.05$; Table 1).

From these nursery habitats, we collected 7507 age-0 red snapper from 536 10-min trawl tows in 1994 and 1995. Significantly more fish were collected in 1995 than in 1994 (ANOVA, $P \leq 0.05$; Fig. 3). Age-0 red snapper first settled to these habitats in late June, showed highest abundance July through September, then steadily declined in the fall of both years (ANOVA, $P \leq 0.05$; Fig. 3). Most fish, 80–81%, were collected at station 1 (ANOVA, $P \leq 0.05$; Fig. 4). At station 1, significantly higher peaks in CPUE ±SE for 1994, were 63.6 ±8.9 in July, 60.8 ±26.2 in August, and 40.3 ±13.4 in September (ANOVA, $P \leq 0.05$). In late August 1995 at station 1, we observed a CPUE (712 ±243) that far exceeded all previous estimates from this study or any previous study. Other significant peaks in CPUE for 1995 at station 1 were 76.2 ±21.4 in mid-August, and 81.4 5.0 in mid-September (ANOVA, $P \leq 0.05$).

Age-0 red snapper ranged from 17.8 to 124.4 mm SL. Fish first settled from the plankton after they reached 17.8 mm SL. The smallest (<20 mm SL) were present both years into mid-September, after which no new settlers were detected (Fig. 5). Significantly higher mean SLs were detected by late August in both years compared with earlier sample periods; size significantly increased with season (ANOVA, $P \leq 0.05$; Table 2; Fig. 5). Fish were significantly larger earlier in 1995, but fish from 1994 caught up in size by September, after which 1994 fish were significantly larger than 1995 fish (ANOVA, $P \leq 0.05$; Table 2; Fig. 5).

In 1994, age-0 red snapper were first abundant (CPUE=63.6) at station 1 and had limited settlement (CPUE=2.0) at station 3 (Fig. 6). Also, fish were significantly larger (ANOVA, $P \leq 0.05$), less abundant, and showed up later at all other stations compared with fish at station 1 in 1994. We did not detect patterns in inshore-offshore movement from fish size, location, and seasonality; we did determine that after first settlement at station 1, fish showed expansion in all directions (Fig. 6). In 1995, new recruits were most abundant in July at station 3 (CPUE=78). After July, patterns were similar to 1994, and most fish were observed at station 1 and fewer larger fish were observed at other stations later in the season (Fig. 7).

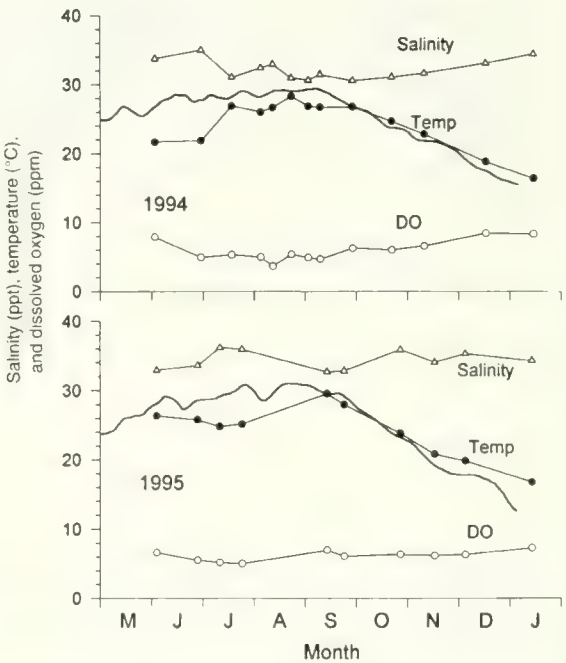

Figure 2

Bottom water temperature (°C), salinity (ppt), and dissolved oxygen (ppm) pooled by stations, in the northeast Gulf of Mexico, from June 1994 to January 1995, and June 1995 to January 1996. Lines without symbols are mean daily surface temperatures based on 10-d moving averages, obtained from a NOAA moored buoy.

The required precision (≤10%), was shown for 57% of all otolith counts (Table 3). Age of red snapper was 26 to 144 days; thus fish may spend up to four months in these habitats. We detected separate late May–June and July cohorts in 1994, and May and June cohorts in 1995, from hatching-date frequencies (Fig. 8).

Growth rates were significantly different among cohorts (ANCOVA, $P \leq 0.05$). The fastest growth rates were observed for June (0.77 mm/d) and July (0.71 mm/d) cohorts in 1994. Growth rates for May (0.51 mm/d) and June (0.67 mm/d) cohorts in 1995 were significantly less than the previous year and significantly different from each other (ANCOVA, $P \leq 0.05$; Fig. 9). Growth rate estimates from SL on varying dates (0.52 mm/d in 1994; 0.62 mm/d in 1995; Fig. 5) were significantly lower than most cohort growth estimates, with the exception of the slow growing May 1995 cohort (ANCOVA, $P \leq 0.05$). In station comparisons for 1995, fish from station 2 had a significantly faster growth rate (0.86 mm/d), followed by fish from station 1 (0.71 mm/d), whereas slower growth rates were observed for station 3 (0.54 mm/d) and station 5 (0.60 mm/d; ANCOVA, $P \leq 0.05$; Table

Table 1

Mean temperatures, mean salinities, mean dissolved oxygen (DO), depths, and +SEs substrate types for trawl stations from the northeast Gulf of Mexico. See Figure 1, for station locations.

Station	Mean temperature (°C)	Mean salinity (ppt)	Mean DO (ppm)	Depth (m)	Substrate type
1994					
1	24.5+1.0	32.7+0.5	5.4+0.4	18.7+0.6	fine sand-shell
2	24.6+1.3	29.9+0.9	6.1+0.5	15.6+0.6	coarse sand
3	24.3+1.4	31.7+0.7	6.1+0.5	13.4+0.6	silt, clay, sand
4	24.9+1.3	32.3+0.5	6.3+0.4	15.0+0.4	coarse sand
5	24.6+1.2	32.7+0.5	6.3+0.4	20.7+0.6	fine sand
1995					
1	24.0+1.2	35.5+0.7	6.3+0.4	19.5+0.1	fine sand-shell
2	25.3+1.2	32.6+0.4	6.2+0.2	16.1+0.7	coarse sand
3	22.6+1.3	33.6+1.3	5.5+0.5	12.7+0.2	silt, clay, sand
4	23.6+1.2	35.6+0.4	6.1+0.2	14.8+0.2	coarse sand
5	23.8+1.3	34.8+0.9	6.5+0.3	20.8+0.2	fine sand

4). Station 4 growth rates were not estimated because of low catch rates.

Discussion

Age-0 red snapper used inner shelf habitat at first settlement, and an area 13 km south of Mobile Bay (station 1) held particularly high numbers. No other study has reported such high CPUEs of age-0 red snapper. Many factors could contribute to this important nursery habitat at station 1. Temperature, dissolved oxygen, salinity, and depths, showed little difference among stations, but one potential aspect that may provide avenues for future studies is substrate type. The substrate in this area may be highly suitable, e.g. relic shell beds (Schroeder et al., 1995) with fine sand sediments, and there is a general shift from shell-sand-mud to "clean" sand east of Mobile Bay,[1] where few fish were collected. Age-0 red snapper may be selecting such shell habitats. For example, age-0 red snapper showed a preference for shell over sand substrata in laboratory studies (Szedlmayer and Howe, 1997)and a preference for almost any small relief structure (e.g. shells) in relation to flat sand substrata in natural habitats (Workman and Foster, 1994). Shells were observed in trawl collections at station 1 and not apparent in trawl samples at other stations. However, we were un-

[1] Hummell, R. L. 1998. Geological survey of Alabama, Tuscaloosa, AL. Personal commun.

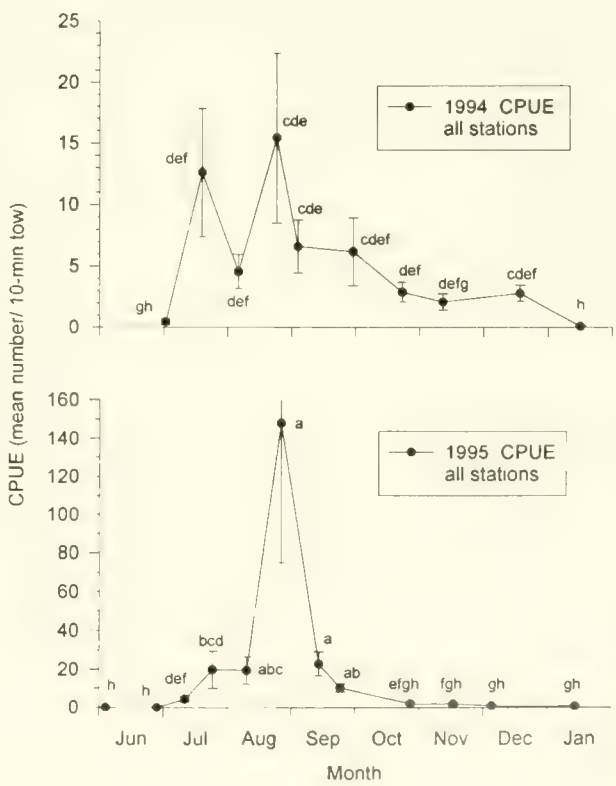

Figure 3

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by date from the northeast Gulf of Mexico. Each point represents mean CPUE for that date. Error bars are standard errors. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P \leq 0.05$).

able to confirm the presence of shell deposits from sediments collected by SCUBA divers.

Red snapper first settled in June, showed peaks in July, August, and September, then quickly declined in numbers from the habitat. There is evidence that this decline of age-0 red snapper from open relatively flat habitats in the fall results from larger age-0 fish migrating to reef structure. In a study of fish recruitment to 1-m^3 concrete artificial reefs, 20 km south of Mobile Bay, age-0 red snapper showed large (up to 89 fish/reef) influxes to these reefs in September and October.[2] This seasonal pattern was similar to the pattern suggested by Holt and Arnold (1982). They found that recruitment of small red snapper to benthic substrate occurred primarily from June through September, and in the fall a few larger age-0 fish were collected by trap near a sunken ship.[3]

Metamorphosis from larva to juvenile is ecologically important in the early life history of fish. In

Table 2

Mean SL (mm) of age-0 red snapper, *Lutjanus campechanus*, for each sample date in 1994 and 1995, from the northeast Gulf of Mexico. Means with different letters show significant differences (ANOVA, Waller-Duncan's test; $P<0.05$).

Date	*n*	Mean SL (mm)	SE
30 June 94	5	25.0[a]	2.01
11 July 94	328	24.1[a]	0.19
1 August 94	121	36.1[c]	0.64
11 August 94	137	26.6[a]	0.72
17 August 94	401	36.1[c]	0.66
30 August 94	165	41.6[d]	1.22
8 September 94	322	42.9[d]	0.46
26 September 94	154	70.5[hg]	1.88
13 October 94	72	75.4[i]	1.59
31 October 94	54	85.9[j]	1.28
14 December 94	42	99.2[k]	3.12
10 January 94	2	116.1[l]	8.35
11 July 95	108	33.2[bc]	0.62
24 July 95	454	31.8[b]	0.40
9 August 95	485	35.5[bc]	0.35
25 August 95	3696	41.1[d]	0.08
12 September 95	572	57.1[e]	0.38
22 September 95	259	66.5[fg]	0.66
25 October 95	53	60.8[e]	2.36
14 November 95	44	72.7[hi]	2.52
2 December 95	18	65.3[f]	4.83
10 January 96	15	89.4[j]	4.67

Table 3

Comparison of otoliths prepared and percent accepted for estimation of age in age-0 red snapper, *Lutjanus campechanus*.

Date	Otoliths prepared	Otoliths with >10% precision	Percent accepted
11 Jul 94	318	172	54
17 Aug 94	316	149	47
8 Sep 94	322	118	37
10–13 Jul 95	108	78	72
9–10 Aug 95	245	180	73
11–13 Sep 95	279	160	57
Total	1588	857	57

[2] Szedlmayer, S. T. 1994. Production or attraction: an evaluation of artificial reefs in coastal Alabama. Alabama Universities Tennessee Valley Research Consortium Final Report, Auburn University, Auburn, AL, 48 p.

[3] Holt, S. A. 1997. Marine Science Institute, Univ. Texas, Port Aransas, TX. Personal commun.

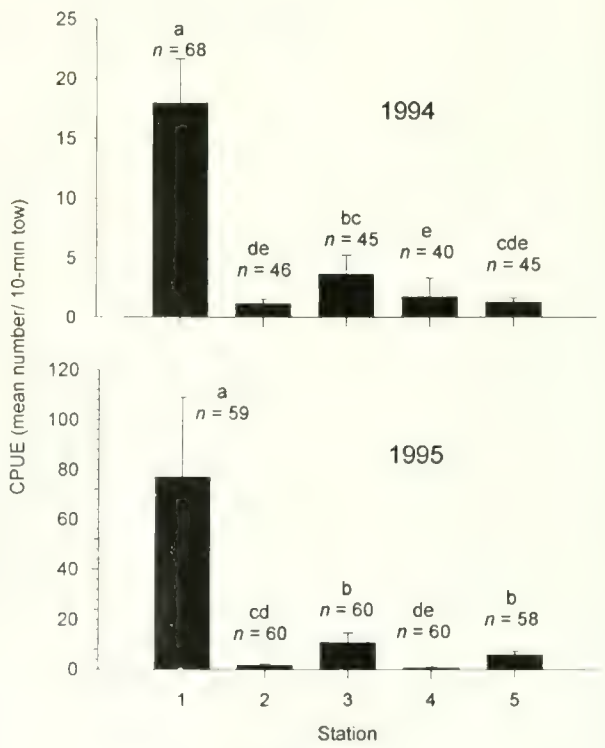

Figure 4

Mean CPUE (number/10-min tow) of age-0 red snapper, *Lutjanus campechanus*, by station from the northeast Gulf of Mexico. Error bars are standard errors, and *n*'s are number of trawl tows. Different letters show significant differences both within and between years (ANOVA; Waller-Duncan test; $P \leq 0.05$).

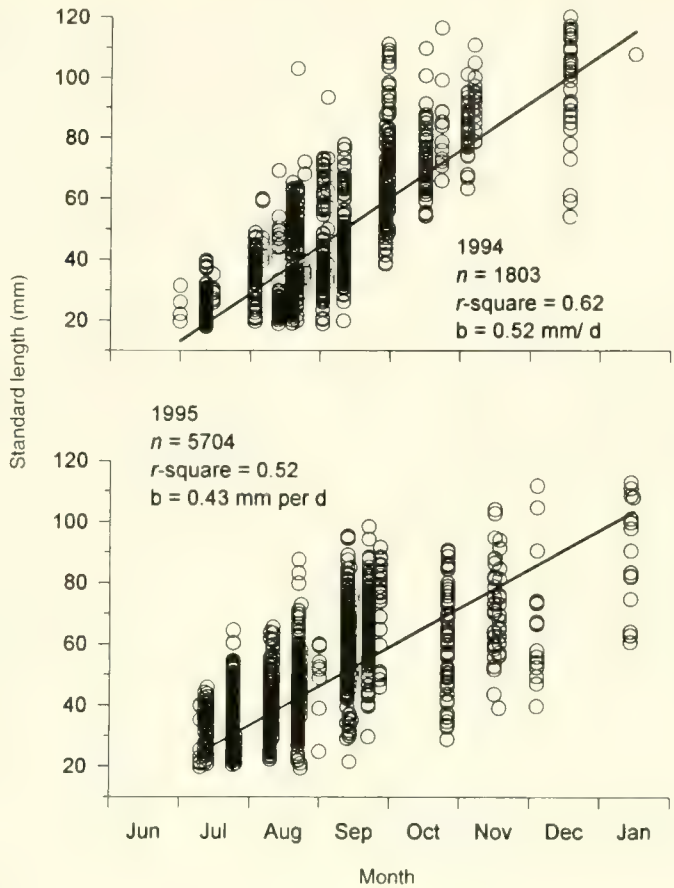

Figure 5

Linear regression of age-0 red snapper, *Lutjanus campechanus*, SL on date for 1994 and 1995, for all fish collected from the northeast Gulf of Mexico. Data points are individual fish. Growth rates were significantly different between years (*t*-test; $P \leq 0.05$).

many fish species this transition occurs simultaneously with habitat change, i.e. from pelagic larvae to benthic juveniles. On the basis of smallest fish collected during this study, larval red snapper metamorphose near 26 d and at 18 mm in length. Collins et al. (1980) suggested similar settlement sizes (12.4 to 22.4 mm SL) from plankton net samples.

Age-0 red snapper otoliths had daily microincrements when growth rates were >0.3 mm/d (Szedlmayer, 1998). In the present study, the nursery period was in the warmer summer months, when food should be abundant; and by all indications, growth rate far exceeded the 0.3 mm/d threshold rate. Thus, back calculation of first increment formation accurately estimated hatching date for age-0 red snapper. One difficulty with the otolith ageing methods was the low (57%) percentage of otoliths that met the required predetermined precision. However, this low percentage was due to personnel skill in otolith preparation. For example, an inexperienced technician would typically over polish several otoliths, that were subsequently rejected when counting. This same technician, after gaining experience and in-

Table 4

Comparison of growth rates among selected stations in 1995. Means with different letters show significant differences (ANCOVA, Tukey's test; $P \leq 0.05$).

Station	Growth rate mm/d	*n*	r^2
1	0.71[a]	227	0.86
2	0.86[b]	25	0.89
3	0.54[c]	115	0.80
5	0.60[c]	49	0.76

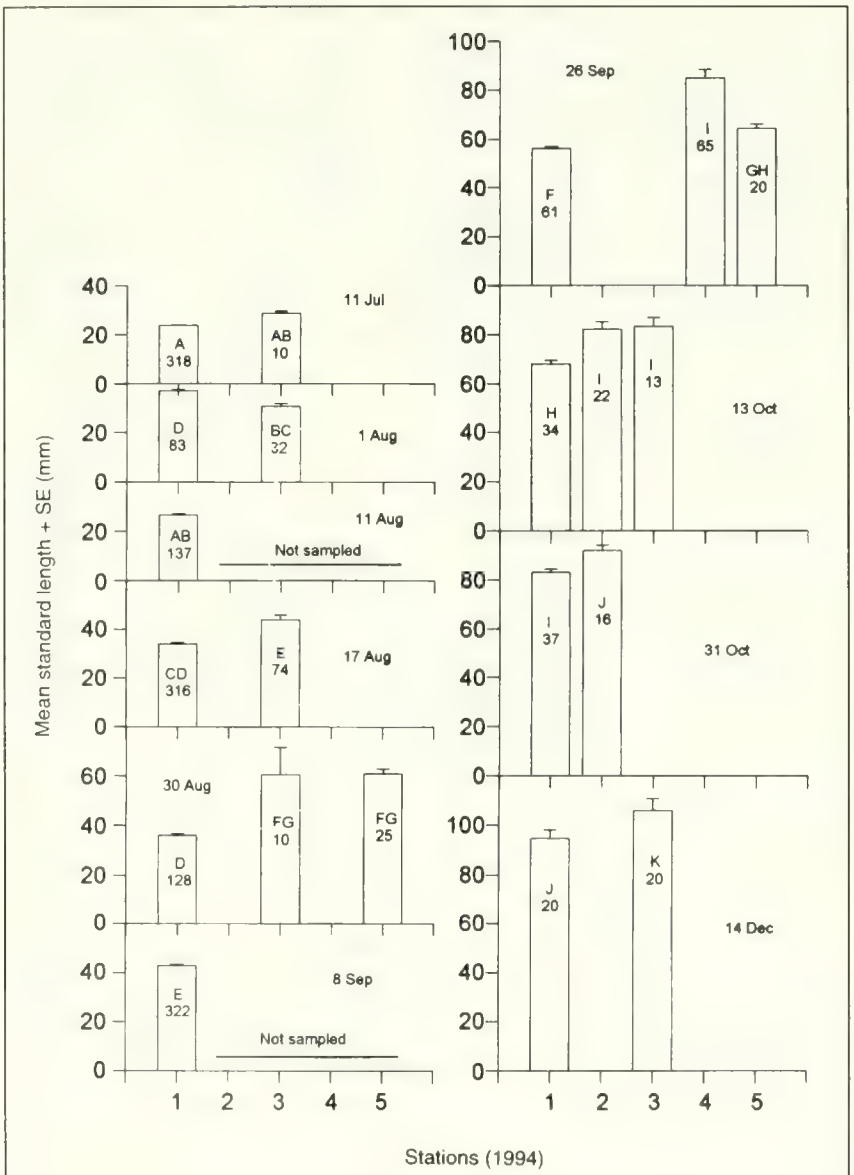

Figure 6

Mean standard lengths by station and date in 1994 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

creased skill, would make an acceptable preparation of the second otolith from the same fish.

Hatching-date distributions clearly indicated separate hatching cohorts with peaks approximately one month apart. The multiple spawnings within a given year in red snapper may be an adaptation to increase survival. By spreading reproductive efforts over time, a species may increase the probability of matching the correct biotic and abiotic conditions for enhanced survival and subsequent recruitment.

Two differences were apparent when hatching-date estimates were compared with estimated spawning periods from gonadosomatic index (GSI) maxima (Collins et al., 1996). First, GSI estimates showed little indication of May spawning, as suggested by May hatching dates in the present study; and second, present estimates showed little indication of August spawning, as indicated by high GSIs for red snapper in August (Collins et al. 1996). These differences between hatch dates and GSIs were probably

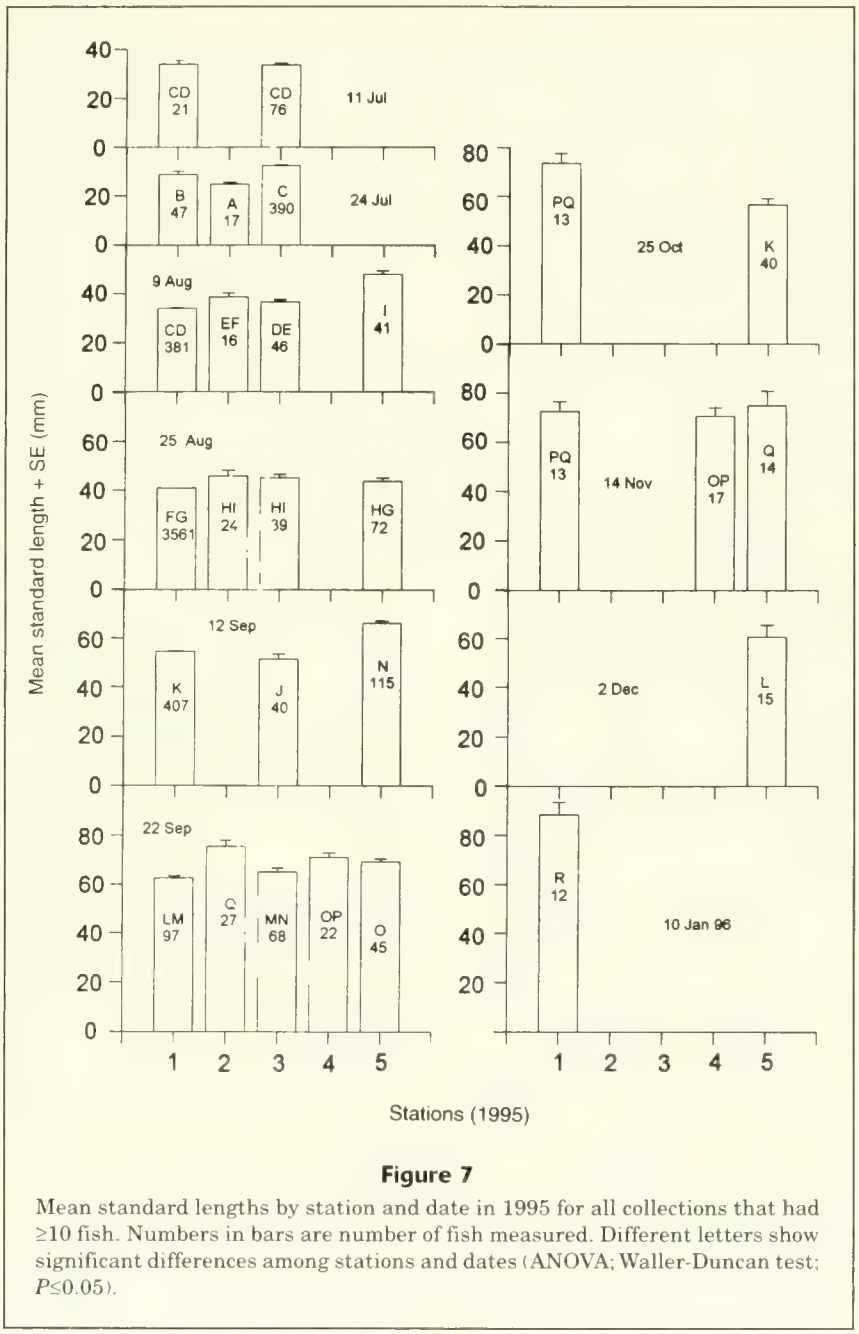

Figure 7

Mean standard lengths by station and date in 1995 for all collections that had ≥10 fish. Numbers in bars are number of fish measured. Different letters show significant differences among stations and dates (ANOVA; Waller-Duncan test; $P \leq 0.05$).

due to yearly variation. Collins et al. (1996) sampled from 1991 to 1993. Lack of evidence for August spawning in our study may also have resulted from low survival of later spawned fish or from new recruits having settled to different habitats not sampled in the present study.

The June and July 1994 cohorts had growth rates that were significantly faster in relation to 1995 cohort growth rates. Growth rates estimated from SL on varying dates were probably inaccurate owing to extended settlement of new recruits, but results showed the same pattern as SL on age estimates, i.e. 1994 growth rates were significantly faster compared with 1995 estimates (t-test, $P \leq 0.05$; Fig. 5). If growth rates were an indication of the probability of survival (Houde, 1989; Sogard, 1997), then 1994 cohorts may have had an advantage over the 1995 spawned cohorts. Growth rate typically decreases with decreasing temperature and may have resulted in the low growth rate observed for the May 1995 cohort. Thus, it appears that both density dependent and density independent mechanisms are operating

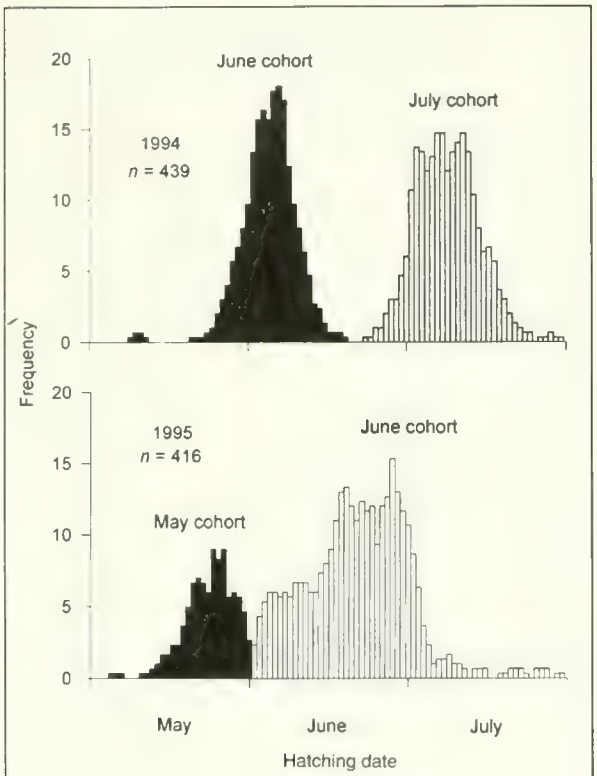

Figure 8

Hatch date frequencies of age-0 red snapper, *Lutjanus campechanus*, pooled over all dates from 1994 and 1995. A three day moving average was applied before plotting.

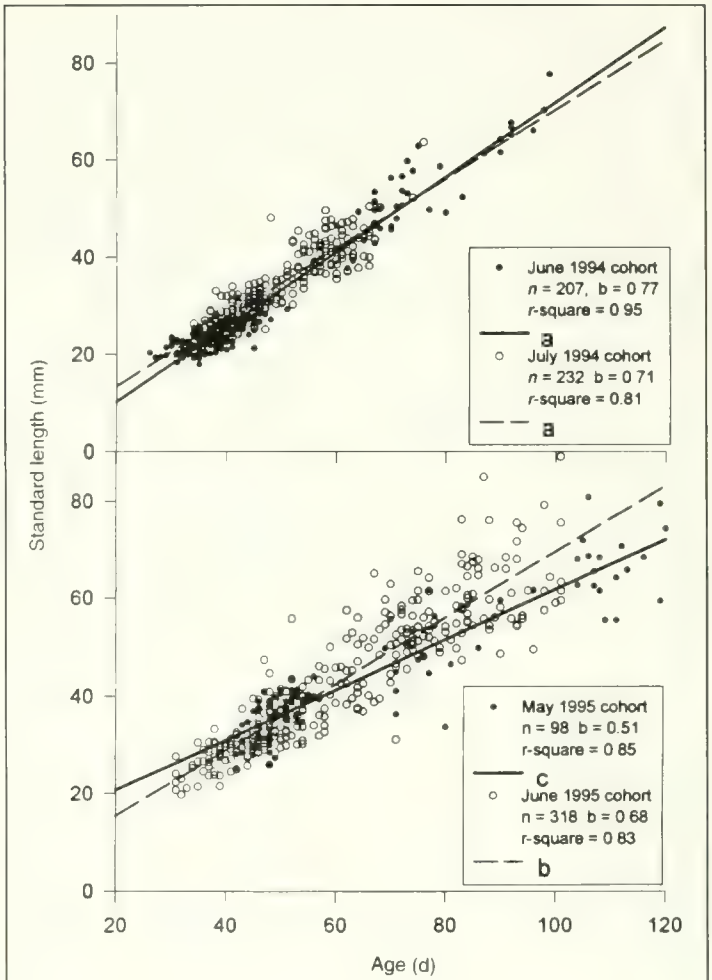

Figure 9

Growth rates of separate cohorts of age-0 red snapper, *Lutjanus campechanus*, from SL on age regressions from the northeast Gulf of Mexico. Data points are individual fish. Different letters show significant differences among cohorts both within and between years (ANCOVA; Tukey's test; $P \leq 0.05$).

(Bromley, 1989; Rijnsdorp and Vanleeuwen, 1992; Rogers, 1994). In 1994, there were fewer fish but faster growth rates than those in 1995, and in 1995 the early May cohort showed the slowest growth rates, probably from colder temperatures. This scenario suggests that if red snapper spawn early (May), temperature may play an important role. As the season progresses into July and August, temperature increases, settlement increases, and competition for food and shelter may become the limiting factors, such that later spawnings in August have lower survival.

The inner shelf habitat in the northeast Gulf of Mexico, particularly the location 13 km south of Mobile Bay, Alabama, should be considered an important nursery area for age-0 red snapper from July through September. Future research should address mechanisms that help to define this red snapper nursery habitat, and back calculation methods could be used to compare the relative contributions of various within-year cohorts to subsequent year classes.

Acknowledgments

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Abstract.—This study examined the relation between statolith and somatic growth in the tropical squid *Sepioteuthis lessoniana*. Five separate linear dimensions were measured on the statoliths of 103 individuals (17–245 mm mantle length). In addition the statoliths of 80 adults (82–245 mm mantle length) were weighed. Statolith increment analysis provided age estimates for 78 individuals. Statolith total length was correlated with age for squid less than ~60 days of age, although neither statolith total length nor weight was a useful predictor of age in older squid. Combining the five statolith dimensions to produce a description of statolith shape provided only slightly better estimates of age than statolith total length or weight alone. Statolith shape changed during ontogeny, developing from relatively elongate juvenile statoliths into the adult form with more robust dorsal and lateral domes. This development was reflected in wider spacing and superior optical definition of daily growth increments in the dorsal and lateral domes of adult statoliths, in relation to the slower growing rostrum. Growth of *S. lessoniana* statoliths does not appear to be strongly linked to mantle growth; both statolith total length and weight increase more slowly than mantle length.

Ontogenetic changes in size and shape of statoliths: implications for age and growth of the short-lived tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae)

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Knowledge of the age structure and growth rates in naturally occurring populations is fundamental to estimating demographic parameters and evaluating ecological processes. Periodic growth increments in squid statoliths are a reliable and accurate tool for determining the age structure of squid populations (Villanueva, 1992; Arkhipkin, 1993; Bigelow, 1994; Jackson, 1994). Growth-rate calculations based on statolith age estimates indicate that tropical squid are short-lived and grow continuously throughout their lifespan (Jackson, 1990; Jackson and Choat, 1992). Growth rates of tropical squid can be strongly influenced by changes in their environment, including temperature fluctuations (Forsythe and Hanlon, 1989), and availability of food (Forsythe, 1993). Consequently, growth rates, final size, and response to changing conditions of tropical squid may vary greatly within or between species (Jackson, 1990; Jackson and Choat, 1992). Apart from obtaining size-at-age information from statoliths, there is also the potential to obtain ecological information on past growth histories of some squid species (Jackson, 1994). Any attempts made at constructing growth histories of squid based on statolith microstructure will benefit greatly from a thorough understanding of growth and development of the statolith and how this relates to growth of somatic tissue.

Daily growth increments in fish otoliths, which are analogous to those in squid statoliths (Radtke, 1983), provide valuable data on the age structure and growth rates of exploited fish species (Campana and Neilson, 1985; Jones, 1986; Stevenson and Campana, 1992). Recent studies of fish somatic-otolith growth relationships may contribute to investigations of somatic-statolith growth relationships in squid. Evidence exists supporting the direct relationship between age and otolith weight for several fish species (Boehlert, 1985; Fletcher, 1991), although further validation is required before otolith weight can be used reliably to estimate age. Several authors have also demonstrated that slower-growing fish have larger otoliths than similar sized, faster-growing individuals (Mosegaard et al., 1988; Secor and Dean, 1989; Wright et al., 1990;

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Mugiya and Tanaka, 1992), indicating a possible disassociation between otolith and somatic growth. Similarly, disassociation between statolith and somatic tissue growth has been demonstrated in the tropical loliginid squid *Loligo chinensis* (Jackson, 1995), and also in two ommastrephid squids, *Todarodes angolensis* and *Todaropsis eblanae* (Lipinski et al., 1993).

The periodic growth increments in squid statoliths are bipartite structures consisting of a discontinuous zone and an incremental zone comprising aragonite ($CaCO_3$) crystals (Lipinski, 1986). Specific morphological differences in the aragonite crystal structure have been illustrated between statolith regions within several squid species (Lipinski, 1993). Crystals of the lateral dome region often display greater variation in shape, size, and orientation than the more homogenous wing crystals (Lipinski, 1993). These variations in crystal structure suggest that accretion is not uniform and that different regions of the statolith may grow at different rates.

The present study provides an assessment of the growth and shape of *Sepioteuthis lessoniana* statoliths based on the linear measurement of statolith dimensions. The potential for using statolith shape descriptions as a proxy for age estimations and the relation between statolith and somatic tissue growth in these squid are examined. Overall descriptions of individual statolith shape covered a broad length and weight range of squid, providing a basis for comparison with age estimates determined by using traditional analysis techniques. With the increased use of statoliths in squid age and growth studies, it is important to understand how statoliths grow and how this growth relates to growth of somatic tissue.

Materials and methods

Study species and collection methods

A total of 103 *Sepioteuthis lessoniana* individuals were captured from waters around the Townsville region of north Queensland, Australia, between January and August 1995. Twenty-three juvenile squid (16–43 mm mantle length [ML]) were captured by using purse seines and dip nets. Juveniles often shelter in surface waters among floating debris or artificially constructed shade devices and are easily netted. Eighty adult squid (82–245 mm ML) were captured from coastal waters at night with squid jigs and by means of light attraction. Individuals were separated into two age groups for these descriptions: juvenile (≤60 days) and adult (>60 days). This separation was based on the techniques used to capture the individuals, which may be related to differences in life style and ecology.

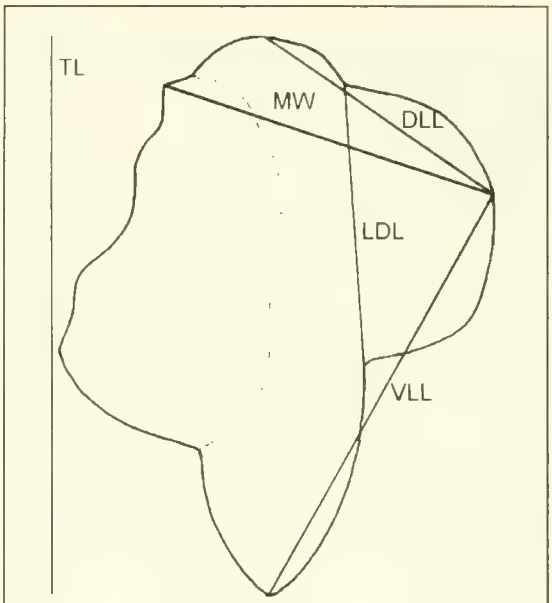

Figure 1

Sepioteuthis lessoniana statolith showing the dimensions measured for morphometric analyses. TL = total statolith length; DLL = dorsolateral length; VLL = ventrolateral length; LDL = lateral dome length; MW = maximum width.

Size measurements

Mantle length was measured from all *Sepioteuthis lessoniana* specimens upon capture. Wet weight was not obtained for the majority of individuals because of the inability to weigh animals accurately on a boat. Statoliths were removed and stored in 70% alcohol, and adult statoliths were later weighed to the nearest 0.01 mg. Weights of juvenile statoliths were not recorded because they were too small to obtain accurate measurements. Five dimensions were measured from each statolith following the descriptions of statolith shape by Clarke (1978): total length, dorsolateral length, ventrolateral length, lateral dome length, and maximum width (Fig. 1). Dimensions were measured from whole statoliths viewed with the anterior (concave) side positioned upward by using an Ikegami-290 high-resolution black and white video camera mounted on a compound microscope. Squid ages were estimated by using statolith increment analysis on ground and polished statoliths (Jackson, 1990). All increment counts were made in the dorsal-dome region of statoliths because increment definition was consistently clearest in this area. Age estimates for 62

adult and 16 juvenile squid were calculated from a mean of three separate counts made by one reader.

Statistical analyses

Paired-sample t-tests indicated no significant difference between left and right statolith total length measures (t=0.67, df=101, P=0.50, n=102), or adult statolith weight measures (t=0.47, df=79, P=0.64, n=80), but wherever possible, the left statolith was used for analyses. For the purpose of this study, statolith "size" refers to the length of each statolith dimension, whereas "shape" indicates that all statolith dimensions have been combined to describe overall statolith structure.

Rates of growth calculated from size-at-age data were not significantly different between adult males and females (Table 1). A size comparison of males and females, adjusted for age, found no significant difference in size between the sexes (Table 2). Individuals were therefore classified as either juveniles or adults, with no distinction made between adult sexes. This classification avoided over-complicating analyses and also provided a larger adult sample size.

Principal components analysis (PCA) was performed on statolith dimensions with the covariance matrix of transformed ($\log_{10}$) data, allowing complete descriptions of statolith shape for all dimensions simultaneously. The magnitude of coefficients in the first eigenvector varies because of changing statolith proportions and relative growth patterns. These coefficients indicate the nature of allometric growth for each variable (dimension) (Jolicoeur, 1963). The coefficients for each variable in the first eigenvector describe the relative growth rates of all the components simultaneously (Shea, 1985). Variables with coefficient scores on the first principal component vector equal to the mean coefficient ($(1/p)^{0.5}$, where p is the number of variables in the analysis) are isometric. Positive and negative allometry is indicated by values greater than and less than the mean coefficient, respectively (Jolicoeur, 1963).

The resampling technique jack-knifing provided means and standard errors (SE) of each coefficient (Marcus, 1990). The probability that the mean coefficient was significantly different from the hypothesized value (Marcus, 1990) is

$$P\left(\begin{array}{c}|mean\ coefficient - hypothesized\ coefficient| \\ > T \times SE \times mean\ coefficient\end{array}\right) < 1/T^2 \quad (1)$$

where T = the number of standard errors for which the probability statement is made.

In this case T = 4.47 provides a probability of 0.05. Simply, the difference between the mean coefficient and the hypothesized coefficient is greater than a critical difference ($T \times$ SE $\times$ calculated coefficient) with a probability $<1/T^2$.

Table 1

Linear regression equations for the size-at-age data of male and female *Sepioteuthis lessoniana*. SE_b = standard error of the slope. *ML*=mantle length (mm). H_o for t-test: b = 0.

Sex	n	Equation	SE_b	r^2	t	P
Male	32	$age = 0.08ML + 5.02$	0.02	0.44	4.84	0.0001
Female	31	$age = 0.08ML + 5.44$	0.02	0.43	4.64	0.0001

Results

Statolith size relationships

The smallest statolith total length (648 μm) was observed in the youngest specimen (17 days old). The largest adult statolith total length (2167 μm) was observed in a 162-day-old mature female, although

Table 2

Analysis of covariance table, comparing mantle length (ML) of male and female *Sepioteuthis lessoniana*, using age as a covariate.

Source	df	Sum of squares	Mean square	F-value	$P > F$
Test for equal slopes					
Sex	1	1.46	1.46	0.32	0.5764
Age (covariate)	1	329.60	329.60	71.21	0.0001
Sex × age (equal slopes)	1	1.20	1.20	0.26	0.6128
Test for differences in ML					
Sex	1	0.40	0.40	0.09	0.7681
Age (covariate)	1	333.23	333.23	73.01	0.0001

the oldest individual was a 186-day-old mature female. Adult statolith weights ranged from 0.29 mg in a 72-day-old immature male to 1.74 mg in a 144-day-old mature female.

Adult statolith weight was not a reliable predictor of squid age, with only 57% (n=62) of the variation in adult ages attributable to weight of the statoliths (Fig. 2A). The strength of the relation between age and statolith total length differed between juvenile and adult squid (Fig. 2B). For juvenile squid, 85% (n=16) of the variation in age was attributable to differences in statolith total length, indicating statolith total length maintains a close correlation with age during the first 60 days of squid growth. In adult squid, the ability to predict age based on statolith total length is poor, and only 57% (n=62) of the variation in squid ages can be explained by statolith length. Statolith total length grew relatively slower than ML for both adult and juvenile squid (Fig. 3A). Adult statolith weight displayed positive allometric growth with ML (Fig. 3B).

Changes in statolith shape

The first PCA axis described 98.6% of the variation among individuals, which is due to statolith shape or the size of all statolith dimensions combined. If we use the PCA score on the first axis as a descriptor of statolith shape, we can account for only 9% and 7% of the variation in statolith total length of juvenile (n=16) and adult (n=78) squid, respectively (Fig. 4B). This result confirms that the first PCA axis contains statolith shape information and not predominantly size information. Growth of the statolith along the total length, ventrolateral and lateral dome axes and in total length was relatively slow, as evidenced by negative allometric growth (Table 3). In contrast, growth of the statolith along the dorsolateral axis and in total width grew relatively faster, as evidenced by the positive allometric growth (Table 3). This finding indicates that the statoliths of juvenile squid are relatively thin and elongate, becoming comparatively

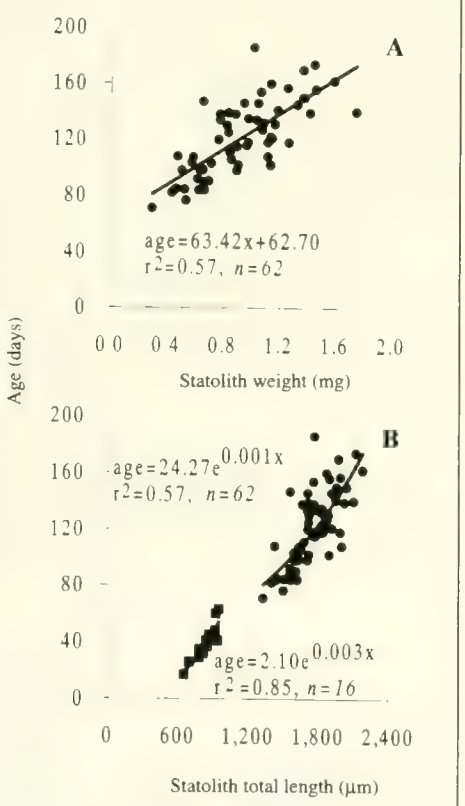

Figure 2

Relationship between (**A**) adult statolith weight and age, and (**B**) statolith total length and age for *Sepioteuthis lessoniana* specimens. Circles = adults; squares = juveniles.

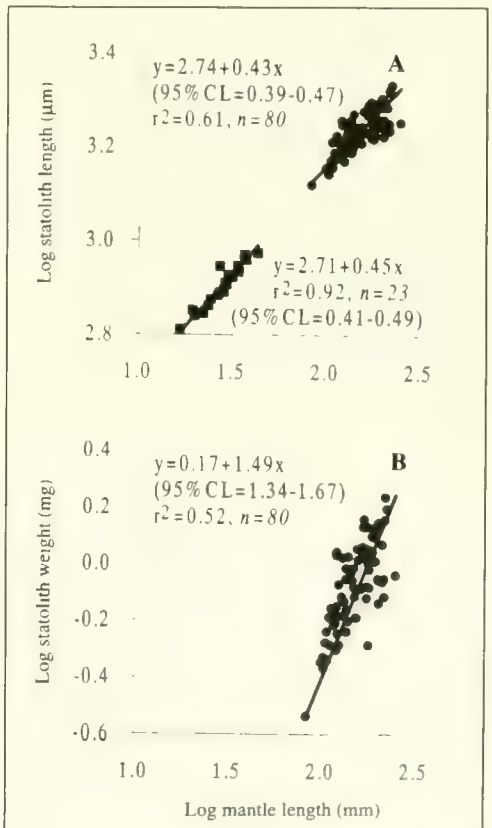

Figure 3

Relation between (**A**) mantle length and statolith total length, and (**B**) mantle length and adult statolith weight for *Sepioteuthis lessoniana* specimens. Circles = adults; squares = juveniles. CL = confidence limits of the slope.

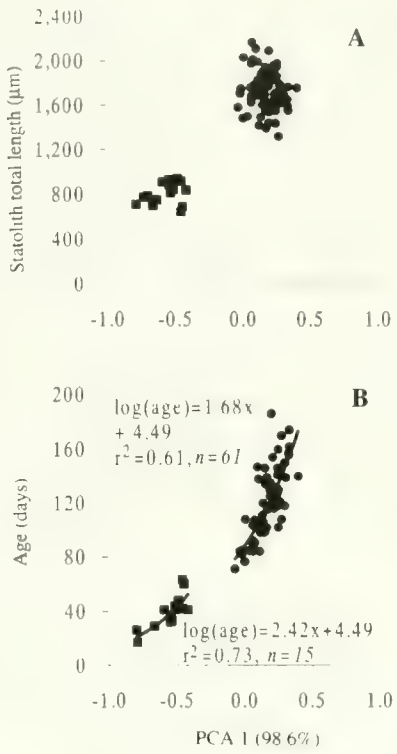

Figure 4

Relative growth of the length of statolith dimensions. The relation between the principal component score on the first axis for each statolith against (**A**) statolith total length, and (**B**) age. The percentages indicate the variation in the data set that has been described by each principal component axis. Circles = adults; squares = juveniles.

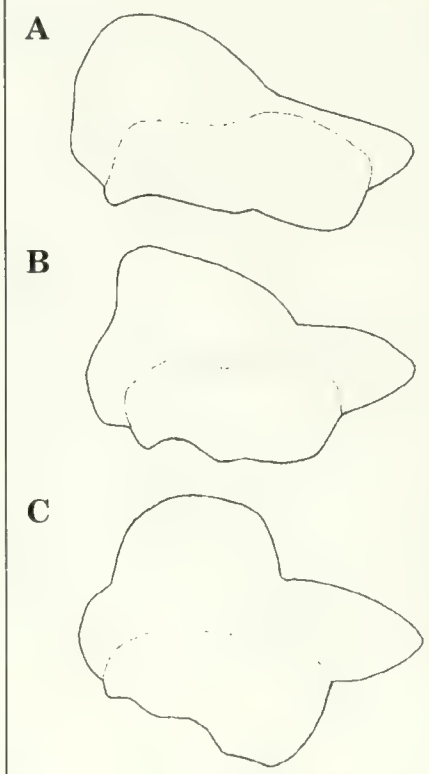

Figure 5

Statoliths of *Sepioteuthis lessoniana*, demonstrating the change in shape from juvenile to adult squid. Mantle lengths and total statolith lengths were (**A**) 16 mm, 648 μm; (**B**) 119 mm, 1525 μm; (**C**) 190 mm, 1875 μm, respectively. Statoliths are shown in anterior view at different scales to facilitate shape comparison.

Table 3

Relative growth of statolith dimensions. Coefficient = coefficient of the first eigenvector. Isometric growth occurs when the coefficient equals $(1/p)^{0.5} = 0.447$. The difference equals the coefficient minus 0.447, which must be greater than the critical difference if allometric growth has occurred; data are $\log_{10}$-transformed; SE = standard errors.

	Coefficient				
Variable	Mean	SE	Critical difference	Difference	Allometric growth
Total length	0.435	0.004	± 0.008	–0.012	negative
Dorsolateral	0.503	0.010	± 0.022	0.056	positive
Ventrolateral	0.387	0.006	± 0.010	–0.060	negative
Lateral dome	0.349	0.005	± 0.008	–0.098	negative
Total width	0.535	0.007	± 0.017	0.088	positive

fatter and bulkier during growth (Fig. 5). Statoliths of the adults continued to grow (Fig. 3); however, there is no relation between the PCA score on the first axis and statolith size for the adults (Fig. 4A), suggesting that the overall shape of individual adult statoliths showed no further change.

Table 4

Relative growth of statolith dimensions. The coefficients for the first three principal component axes (PCA) of the analysis on length variables; data are $\log_{10}$-transformed and the covariance matrix was used.

	Eigenvector		
Variable	PCA 1	PCA 2	PCA 3
Total length	0.435	0.308	0.154
Dorsolateral	0.503	−0.695	0.321
Ventrolateral	0.387	0.592	−0.108
Lateral dome	0.349	0.210	0.579
Total width	0.535	−0.163	−0.726

Additional variation in statolith shape described on the second and third PCA axes was attributable to differences among juvenile, rather than adult squid (Fig. 6, A and B: Table 4). Growth of the statolith along the ventrolateral and lateral dome axes and in total length were all important as statoliths approached their final size and shape. The ventrolateral and total lengths were proportionally larger in juveniles, whereas the dorsolateral length and total width were proportionally smaller immediately before individual statoliths attained their final adult shape.

If the PCA score of each individual statolith on the first axis, as a descriptor of shape, is used to estimate age of the squid, then an improved correlation between age and statolith shape is seen when compared to the correlation between age and statolith total length alone (juveniles n=15, r^2=0.73; adults n=61, r^2=0.61) (Fig. 4B). There is an exponential relationship for both juvenile and adult squid but changes in statolith shape slow in older individuals. Analysis of adult and juvenile statoliths as separate groups to eliminate gross statolith size differences that were identified in the PCA only highlighted the overall variability in statolith shape within the two age groups, particularly among adult squid.

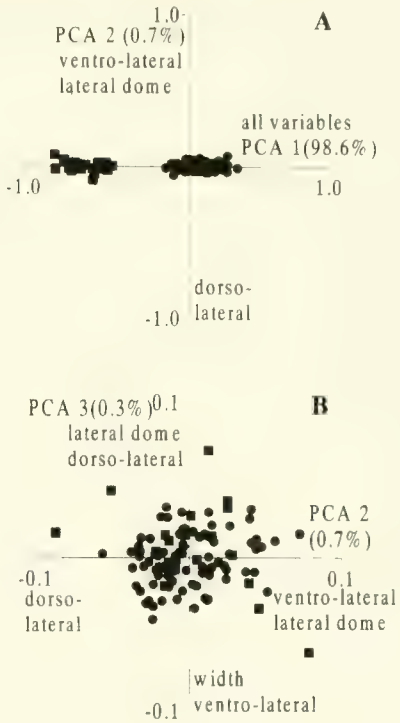

Figure 6

Relative growth of the length of statolith dimensions. Principal component scores for the length of five statolith dimensions on the first three axes. The percentages indicate how much variation in the data set has been described by each principal component axis. Data are $\log_{10}$ transformed. Circles = adults; squares = juveniles.

Discussion

Results from this study suggest that neither statolith total length nor weight measurements can be reliably used to predict the age of a *Sepioteuthis lessoniana* individual. Statolith total length is a reasonable predictor of age for juvenile squid (less than 60 days old) but cannot be used to predict age in older individuals of this species. This conclusion is in contrast with that of González et al. (1996) who observed that statolith length in *Illex coindetti* shows significant dependence on age (males n=170, r^2=0.71; females n=171, r^2=0.74). However, they also suggested that the use of statolith length for age estimations would require verification over several years to confirm this relationship. Statolith length has also been shown to reflect age in *Illex illecebrosus* females (n=31, r^2=0.96) (Morris and Aldrich, 1985), whereas statolith weight provided a better reflection of age (n=112, r^2=0.88) than statolith total length in *Todarodes angolensis* (Villanueva, 1992). Even combining all five statolith dimensions to produce a description of statolith shape in this study provided only marginally better age estimates for *S. lessoniana* individuals than statolith total length or weight measurements alone.

Variation was evident in size between adult statoliths in this study because the heaviest statoliths did not necessarily possess the longest total lengths. Additionally, as much as half of the variation in statolith total lengths was not attributable to age of the

individuals. This indicates a disassociation between statolith and somatic (mantle length) growth in *S. lessoniana*. The disassociation of otolith and somatic growth has been demonstrated in several fish species (e.g. Mosegaard et al., 1988; Secor and Dean, 1989; Francis et al., 1993). In squids, *Loligo chinensis* (Jackson, 1995), and *Todaropsis eblanae* and *Todarodes angolensis* (Lipinski et al., 1993) also display disassociation between statolith and somatic tissue growth. Comparison of statolith size and shape between *Todarodes angolensis* and *Todaropsis eblanae* also has revealed distinct species differences (Lipinski et al., 1993). Jackson (1995) suggested that the use of the relation of statolith length to mantle length as a predictor of squid ages should proceed with caution until temperature-related effects on squid growth (e.g. seasonal effects), as well as the relation between statolith and somatic growth are better understood.

The disassociation between statolith and somatic growth rates is possibly a function of differences between the mechanisms responsible for these two processes. A process related to metabolic rate, rather than somatic growth, seems to govern the rate of otolith accretion in fish (Wright, 1991). Although a close correlation often exists between fish somatic growth and metabolic rate in early life-history stages, intrinsic or extrinsic constraints on somatic growth may affect this relationship and result in a disassociation between otolith and somatic growth (Wright, 1991). Recently, Lombarte and Lleonart (1993) proposed that otolith growth in fish may occur under dual regulation: overall shape is genetically determined whereas otolith size is governed by environmental factors. Several workers have also suggested that temperature plays a particularly important role in determining otolith growth, primarily through the effect of temperature on metabolic rate (Wright, 1991; Bradford and Geen, 1992). In order to demonstrate a link between otolith and somatic growth rates the age-independent variability in the relationship needs to be assessed (Hare and Cowen, 1995). The mechanisms governing statolith growth in *S. lessoniana* remain to be determined but may possibly be related to the high plasticity of somatic growth and a fixed growth trajectory of the statolith. Ontogenetic behavioral adaptations may also play a key role. Nonetheless, there are important considerations for age and growth studies based on the morphological features of statoliths; whereas many squid are known to grow continuously throughout their life (Jackson and Choat, 1992; Jackson, 1994), growth of statoliths in our study appears to approach a final asymptotic size and shape. Statoliths grow with the age of the squid, but statolith accretion may respond differently to environmental factors than to growth of somatic tissue.

The breakdown in the relation between statolith total length and age in older *S. lessoniana* individuals may be attributed to variable accretion rates in the statoliths of adult squid, possibly in relation to environmental conditions. Varying aragonite accretion within statoliths could bring about fluctuations in daily increment widths that ultimately lead to differences in overall length and weight of similar aged statoliths. These differences are likely to be more detectable in the older, larger statoliths of adult squid. Alterations in otolith increment widths leading to different sized otoliths of the same age have been shown for several fish species in response to both biotic and abiotic factors (e.g. Eckmann and Rey, 1987; Sogard, 1991; Burke et al., 1993). Further work on other fish species has shown that changes in increment width may lag or be unrelated to changes in somatic growth (Molony and Choat, 1990; Milicich and Choat, 1992). Variable statolith increment widths, that may be attributable to environmental conditions, have been shown in at least one squid species (*Abralia trigonura*, Bigelow, 1992), and one cuttlefish (*Sepia hierredda*, Raya et al. 1994).

Modifications of otolith shape and daily increment structure in fish have been attributed to environmental changes or fluctuations in individual fish physiology (Morales-Nin, 1987; Nishimura, 1993; Wright, 1993; Tzeng and Tsai, 1994). As some fish migrate, modifications are often necessary in order to meet unique requirements for balance, orientation, and navigation (Blaxter, 1988). A transformation of otolith shape may occur, resulting in discontinuities and secondary growth structures (Sogard, 1991; Hare and Cowen, 1994). Statoliths are the major sensory structure responsible for balance and orientation of squid (Budelmann, 1990). The shape and structure of the statocyst chamber itself are important to the swimming performance and sensory perception capabilities of cephalopods (Williamson, 1991). Statolith shape and structure is, therefore, also likely to affect the response of this unique and complex sensory organ. Although *S. lessoniana* does not display distinct life-style changes or habitat shifts, a transition from the observed juvenile habitat, where it commonly shelters among floating surface debris, to an adult lifestyle that is typically more reef-associated, may involve behavioral adaptations that lead to differential growth of statoliths. Knowledge of the mechanism by which this growth occurs and how it can be modified during ontogeny will be critical to understanding how statoliths grow.

Most growth of adult statoliths in this study occurred in the dorsal and lateral dome regions, producing a more rounded and bulkier form than that of the juveniles. The negative allometric growth in

total length and along the lateral dome and ventrolateral length axes suggests that relative growth of these regions is slow and that statoliths retain the elongate region of the rostrum as they grow. This was reflected in the superior definition and clarity of daily increment structures in the lateral dome region of adult statoliths when viewed under a light microscope. This may also explain why optical acuity of daily increment structures in the rostrum region of adult statoliths was poor. Slower growth of statoliths in the rostrum indicates deposition of less aragonite material compared with other faster growing regions of the statolith and in turn suggests that daily increment widths in the rostrum will be narrower and therefore harder to discern with light microscopy. In contrast, daily growth increments have been reported as displaying optimal definition in the rostrum of two other squid species (*Photololigo edulis*, Natsukari et al., 1988; *Berryteuthis magister*, Natsukari et al., 1993). Therefore, it is likely that differences occur in statolith accretion between species, possibly related to behavior. Optical definition of daily increments in statoliths has important consequences when ageing and growth studies are based on counts and distances between increments. Age and growth calculations based on narrower less distinct increments may not reveal true patterns otherwise evident in optically more distinct incrementation.

Results from this study suggest that prediction of age of *S. lessoniana* individuals from the size and shape of their statoliths remains doubtful on account of the disassociation between statolith and somatic tissue growth. Changes in statolith shape during growth may also be important if statoliths are to be employed as a tool for constructing growth histories of *S. lessoniana*. Variable levels of statolith accretion ultimately leading to slight modifications in shape may not necessarily be indicative of changes in somatic growth. Ageing studies based on analyses of statolith size from other squid species need to be aware of the possible disassociation between statolith and somatic tissue growth. The changes in size and shape of *Sepioteuthis lessoniana* statoliths described in this study are likely due to differing aragonite accretion levels, possibly on a daily basis, in response to physiological and behavioral adaptations during ontogeny.

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Differential habitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California

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Abstract.—Economically valuable California halibut, *Paralichthys californicus*, and barred sand bass, *Paralabrax nebulifer*, along with other fishes, are often abundant in the shallow areas of California bays during their early life history. However, little is known about their habitat use within these areas. We investigated habitat use of juvenile fishes in the shallow waters of an embayment by towing a 1.6-m beam trawl with 3-mm mesh through eelgrass beds (*Zostera marina*) and unvegetated areas at depths ≤1.1 m in Alamitos Bay. Tows were conducted monthly or bimonthly from May 1992 through November 1995. A total of 435 tows during 31 months yielded 52,787 fishes comprising 46 species. However, the catch was dominated by only a few species and consisted mostly of juveniles and gobiid larvae. A total of 1157 California halibut and 225 barred sand bass were collected. California halibut were 2–6 times more abundant in unvegetated areas than in eelgrass beds, whereas barred sand bass were captured almost exclusively in eelgrass. Abundance of both species significantly decreased as distance from the bay mouth increased. Abundances of most other fishes also varied considerably between habitats and among sites. In contrast to California halibut and barred sand bass, abundances of other species were higher at sites farther inside the bay. Variations in water temperature, dissolved oxygen, salinity, eelgrass shoot density, and eelgrass blade length failed to explain differences in abundance for most fishes. Habitat and site selection for juvenile California halibut and barred sand bass may be related to larval supply and to the first suitable area encountered, but may be modified subsequently by movement into other areas in search of preferred food items.

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It is widely recognized that bays and estuaries are important nursery grounds for many marine species. Within these areas, numerous studies have documented the importance of eelgrass, *Zostera marina*, and other seagrasses as habitat for fishes. The composition and abundance of fishes in these habitats can vary considerably from unvegetated areas (Orth and Heck, 1980; Borton, 1982; reviewed in Orth et al., 1984; Heck et al., 1989; Ferrell and Bell, 1991; Sogard and Able, 1991). Seagrass habitats may be important because of their associated food resources or because they provide a refuge from predation (Adams, 1976; Heck and Thoman, 1981; reviewed in Orth et al., 1984; Leber, 1985; Sogard and Olla, 1993).

The association of fishes with seagrass beds has been related to various physical characteristics of seagrass, such as shoot density, blade length, and biomass (Adams, 1976; Orth and Heck, 1980; reviewed in Orth et al., 1984; Bell and Westoby, 1986a). However, evidence suggests that physical characteristics of seagrasses may only affect fish abundances on a local scale such as within a seagrass bed, but not over larger scales such as different beds within a bay (Bell and Westoby, 1986b; Bell et al., 1988; Sogard, 1989; Worthington et al., 1992). Instead, it has been suggested that differing fish abundances in seagrass beds across an estuary are due to availability of competent larvae; pelagic larvae of some seagrass fishes settle indiscriminately in the first seagrass bed encountered regardless of seagrass physical characteristics (Bell and Westoby, 1986b; Bell et al., 1987, 1988). According to this "settle and stay" hypothesis, once within a seagrass bed, fishes would move around selecting microsites but would not leave the seagrass bed because of greater predation risks associated with moving over unvegetated substrata. However, others have found that initial settlement patterns in habitats may be altered considerably by postsettlement mortality (Levin, 1994), migration to other areas (Sogard, 1989), or by both in response to available food (Jenkins et al., 1996).

Much of the work on seagrasses and associated fishes has taken place on the east coast of the United States or in other parts of the world. Although several studies have described the ichthyofauna of southern California bays (Allen and Horn, 1975; Horn and Allen, 1976; Allen, 1982; Allen and Herbinson, 1991), few studies have described the relation of fishes with eelgrass and other habitats. Understanding

these relationships within bays is particularly important owing to the destruction and severe alteration of about 75% of coastal estuary and wetland habitats in southern California since 1900 (California Coastal Zone Conservation Commissions, 1975). Reduced catches of California halibut, *Paralichthys californicus*, may be due to the alteration or loss of this nursery habitat within bays and estuaries, or to both (Plummer et al., 1983; Kramer and Sunada, 1992; Kramer and Hunter[1]).

California halibut is an important commercial and sport fish in southern and central California. Barred sand bass, *Paralabrax nebulifer*, is also an important sport fish in southern California and ranks annually among the top three species caught aboard commercial passenger fishing vessels (Love et al., 1996a). Both of these fishes spawn in nearshore waters (Frey, 1971; Ono, 1992) and occupy embayments during their early life history; newly settled and larger juvenile California halibut are frequently found over shallow, sandy substrata (Haaker, 1975; Allen, 1988; Allen and Herbinson, 1990, 1991; Kramer, 1990, 1991a, 1991b), whereas juvenile barred sand bass are found in eelgrass beds (Feder et al., 1974; Rosales-Casián, 1997). However, little additional information is available on habitat use by these and other fishes within these areas.

Therefore, the purpose of our study was to determine 1) if abundances of juvenile California halibut, barred sand bass, and other fishes differed between eelgrass and unvegetated habitats, 2) whether these abundances differed among sites within the bay, and 3) whether these differences were related to physical characteristics of eelgrass or abiotic factors. We examined habitat use by collecting fishes with a beam trawl towed in shallow eelgrass beds and nearby unvegetated areas at three sites within a single bay. A beam trawl was used because it collects smaller halibut and other flatfishes more effectively than beach seines and otter trawls (Gunderson and Ellis, 1986; Kramer, 1990; Kuipers et al., 1992) and allows comparison with other studies where similar gear was used.

Materials and methods

Study area and sampling

Our study was conducted in Alamitos Bay (lat. 33°45'N, long. 118°07'W), which is a small embayment located at the southeastern boundary of Los Angeles County in southern California. Alamitos Bay was once an estuary of tidal marshes and mud flats. It has been considerably modified by dredging, filling, and construction of homes, marinas, and two jetties that mark the entrance. The bay is exposed to semidiurnal tides with a mean range of 1.1 m. Water circulation is further enhanced by large amounts of water drawn by two power stations that flush the bay every 19 hours (Phillips[2]). Regardless of tidal flux, there is a consistent flow of water into the bay (Brown and Caldwell[3]).

Sampling was conducted at three sites (Bay Entrance, Belmont Shore, and Marine Stadium) separated by at least one km (Fig. 1). At each site, sampling occurred in two habitats, eelgrass (*Zostera marina*) beds and nearby unvegetated sandy-mud areas located about 40 m away. A weighted 1.6-m beam trawl, equipped with skis, tickler chain, and 3.0-mm stretched-mesh netting, was towed parallel to shore by two people on foot at low tide during the lowest tides of the month. Tows were made during daylight hours at depths from 0.3 m to 1.1 m, lasted 90 seconds, and covered approximately 56 m^2. We completed 2–5 tows, depending on tide height, in each habitat at each site over four consecutive days. Sampling was conducted monthly from May 1992 through April 1993 (excluding February) and from November 1993 through December 1994. Bimonthly sampling occurred from January 1995 through November 1995. All fishes were sorted, identified, counted, and returned to the water. Most fishes were measured to the nearest mm standard length (SL) from May 1992 through October 1994, whereas California halibut and barred sand bass were measured throughout the study. Although California halibut and barred sand bass undergo transformation at about 7–9 mm SL and 11 mm SL, respectively (Butler et al., 1982; Ahlstrom et al., 1984; Gadomski et al., 1990), all individuals ≤20 mm SL were considered to be "newly settled" or "newly recruited" (Allen and Herbinson, 1990; Kramer, 1990; Love et al., 1996b). Larval and postlarval gobies (Brothers, 1975) that were not identified further were classified as "goby larvae." Other fishes not sexually mature based on size at first maturity information were considered to be juveniles. Water temperature, dissolved oxygen, and salinity data were collected for most tows,

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[2] Phillips, K. W. 1978. A water and sediment study of Alamitos Bay correlated with peak and minimal recreational aquatic activities. City of Long Beach Chemical and Physical Testing Laboratory, Long Beach, California. Unpubl. data.

[3] Brown and Caldwell Environmental Sciences Division. 1979. Embayment ecology studies: physical oceanographic and water quality data report. Southern California Edison. Unpubl. data.

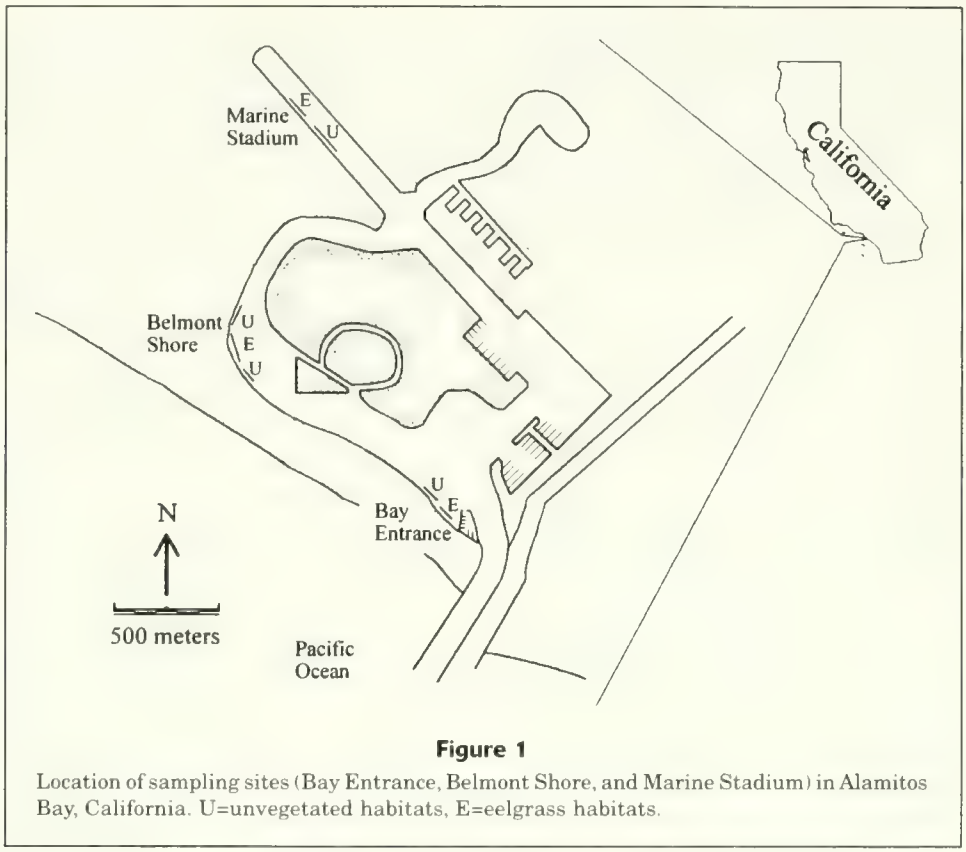

Figure 1

Location of sampling sites (Bay Entrance, Belmont Shore, and Marine Stadium) in Alamitos Bay, California. U=unvegetated habitats, E=eelgrass habitats.

except during September 1994 through December 1994, when dissolved oxygen values were not taken owing to equipment failure. Bottom water temperature and dissolved oxygen were recorded with a YSI Model 51B oxygen meter. Surface salinity was measured with a temperature-compensated refractometer.

Eelgrass bed length, bed width, shoot density, and blade lengths were measured by two divers using SCUBA. A 300-m transect tape was laid out in the center of the bed along its longest axis. Width was measured perpendicular to the tape at three equidistant points. Divers sampled 1/16 m^2 quadrats in the bed at predetermined random points perpendicular to the tape. Within each quadrat, all shoots were counted and the lengths of two randomly selected blades were measured. A total of 10–20 quadrats were sampled at each site during August 1992, March 1993, December 1993, and December 1995.

Data analysis

Nonparametric statistics were used because data and their transformations were heteroscedastic and not normally distributed. A nonparametric two-factor analysis of variance (ANOVA) on ranked data (Zar, 1984) was performed separately on the number of California halibut, barred sand bass, and 13 other common fishes captured per tow with habitat and site as factors. If significant main effects with no significant interactions were found, Tukey-Kramer multiple comparisons were performed to determine which pairs of means were significantly different. The results were considered significant if P was <0.05. If significant interactions between habitat and site were found, analyses of main effects were considered dubious and subsets of data were formed for each level of one factor within each level of the other factor and *vice-versa* (Underwood, 1981). Kruskal-Wallis and Dunn multiple comparisons (Hollander and Wolfe, 1973) were performed on these subsets. For example, a Kruskal-Wallis test was used to determine if there was an overall difference in abundance among sites for unvegetated habitats, and then for eelgrass habitats. If a significant difference was found, Dunn multiple comparisons were made to determine which pairs of sites were significantly different. For fishes other than California halibut and barred sand bass, comparisons among sites were made only for the habitat where they were most abundant overall. Abundance differences between habitats were determined by a Wilcoxon two-sample test on unvegetated and eelgrass habitat data within each site.

Two-sample Kolmogorov-Smirnov tests were used to compare length-frequency distributions between

Table 1

Physical characteristics of eelgrass (*Zostera marina*) at three sites in Alamitos Bay. Data were collected in August 1992, March 1993, December 1993, and December 1995. Values represent mean ± one standard error. Sample sizes for bed length and width measurements were 4 and 12, respectively. Sample sizes for density: Bay Entrance=79, Belmont Shore=70, and Marine Stadium=80. Sample sizes for blade length: Bay Entrance=154, Belmont Shore=138, and Marine Stadium=155.

Site	Bed length (m)	Bed width (m)	Density (no. shoots per quadrat)	Blade length (cm)
Bay Entrance	82.9 ± 18.6	16.3 ± 2.9	10.1 ± 0.5	68.3 ± 2.2
Belmont Shore	102.9 ± 2.5	8.8 ± 0.3	7.9 ± 0.5	37.2 ± 1.5
Marine Stadium	54.1 ± 5.9	15.8 ± 1.3	10.6 ± 0.7	47.9 ± 1.9

habitats and sites for California halibut and barred sand bass. Subsets of these data (see above) were used in these analyses.

Kruskal-Wallis and Dunn multiple comparisons were also made on the mean number of eelgrass shoots and mean blade length per quadrat to determine differences in these eelgrass characteristics among the three sites. Water temperature, dissolved oxygen, and salinity values for each tow were used in a two-way nonparametric ANOVA to test for differences in each of these abiotic factors between habitats and among sites.

Results

Eelgrass characteristics and abiotic factors

Physical characteristics of eelgrass beds at the three sites were very different. Belmont Shore had the longest bed but mean bed width, eelgrass shoot density, and eelgrass blade length were lowest (Table 1). Eelgrass densities at Bay Entrance and Marine Stadium were significantly greater than at Belmont Shore ($P<0.05$), and all blade length comparisons among sites were significantly different ($P<0.05$).

Abiotic factors varied temporally but showed little spatial variation. Mean monthly values ranged from 14.5 to 23.0°C for water temperature, 4.8–8.1 mg/L for dissolved oxygen, and 23.2–36.0 ppt for salinity. These abiotic factors were very similar between habitats and among sites except for slightly lower dissolved oxygen in eelgrass and higher water temperatures at Marine Stadium. However, none of these abiotic factors were significantly different between habitats or among sites ($P>0.05$).

Fish community

A total of 52,787 fish representing 46 species was collected from 435 tows (Table 2). The catch was dominated by a few species that were often captured in large numbers.

Numbers of species varied among habitats and sites. Many more species were captured in eelgrass beds ($n=42$) than in unvegetated areas ($n=26$). We collected 19 species exclusively in eelgrass beds but captured only three species solely in unvegetated areas (Table 2). Species numbers decreased as distance from the bay mouth increased; more species were collected at Bay Entrance ($n=40$) than at Belmont Shore ($n=35$) and Marine Stadium ($n=28$).

California halibut

California halibut ranked eighth in abundance; 1157 individuals were collected from 50.8% of the tows (Table 2). The number of California halibut captured per tow ranged from 0 to 81 with a mean of 2.7 ± 0.32 SE. The abundance of newly settled California halibut was greatest from March through May (Fig. 2). A total of 325 newly settled California halibut was captured. For all sites and habitats combined, maximum mean density per month of newly settled individuals was 15/100 m^2 (May 1995). Maximum mean density per month at an individual site and habitat was 81/100 m^2 (May 1995, Bay Entrance unvegetated area).

California halibut abundance varied considerably among habitats and sites (Fig. 3A). The magnitude of these differences depended upon the habitat and site as indicated by a significant interaction term in the two-way ANOVA ($P=0.002$). Abundance was significantly different between habitats at all three sites, for all three site comparisons in unvegetated areas, and for two of three comparisons in eelgrass beds (Table 3). Within sites, Marine Stadium and Belmont Shore unvegetated areas contained about 2–3 times as many California halibut as eelgrass beds, and Bay Entrance unvegetated area had more than six times as many California halibut as nearby eelgrass (Fig. 3A). Within both habitats, California

Table 2

Total number of fishes captured by habitat type and frequency of occurrence in Alamitos Bay, California, from May 1992 through November 1995.

Common name	Scientific name	Unvegetated habitat n=251	Eelgrass habitat n=184	Total number captured	Frequency of occurrence (%) n=435
Goby larvae	unidentified Gobiidae	6491	10336	16827	57.7
Cheekspot goby	*Ilypnus gilberti*	8836	1009	9845	74.9
Bay pipefish	*Syngnathus leptorhynchus*	70	8203	8273	49.0
Shiner perch	*Cymatogaster aggregata*	5	4121	4126	23.2
Topsmelt	*Atherinops affinis*	2463	1163	3626	33.1
Giant kelpfish	*Heterostichus rostratus*	9	2454	2463	36.8
Arrow goby	*Clevelandia ios*	1216	840	2056	18.6
California halibut	*Paralichthys californicus*	1024	133	1157	50.8
Queenfish	*Seriphus politus*	662	253	915	13.1
Diamond turbot	*Hypsopsetta guttulata*	625	53	678	37.9
Spotted kelpfish	*Gibbonsia elegans*	1	478	479	19.3
Shadow goby	*Quietula y-cauda*	20	394	414	12.9
Pacific staghorn sculpin	*Leptocottus armatus*	241	129	370	37.0
Bay blenny	*Hypsoblennius gentilis*	3	326	329	20.5
Barred sand bass	*Paralabrax nebulifer*	4	221	225	12.4
Salema	*Xenistius californiensis*	0	180	180	4.6
California killifish	*Fundulus parvipinnis*	42	128	170	8.5
Black perch	*Embiotoca jacksoni*	0	86	86	5.3
Sargo	*Anisotremus davidsonii*	0	86	86	3.7
Spotted turbot	*Pleuronichthys ritteri*	54	12	66	8.7
Kelp bass	*Paralabrax clathratus*	0	56	56	6.7
Snubnose pipefish	*Cosmocampus arctus*	2	46	48	7.4
California clingfish	*Gobiesox rhessodon*	4	41	45	5.1
Black croaker	*Cheilotrema saturnum*	0	42	42	4.4
Mussel blenny	*Hypsoblennius jenkinsi*	7	35	42	3.9
Spotted sand bass	*Paralabrax maculatofasciatus*	0	38	38	4.6
Reef finspot	*Paraclinus integripinnis*	0	30	30	3.2
Dwarf surfperch	*Micrometrus minimus*	0	28	28	2.5
Yellowfin goby	*Acanthogobius flavimanus*	8	8	16	2.8
Mozambique tilapia	*Tilapia mossambica*	0	14	14	2.1
Blenny larvae	*Hypsoblennius* spp.	0	9	9	1.2
California tonguefish	*Symphurus atricauda*	3	5	8	1.4
California scorpionfish	*Scorpaena guttata*	0	6	6	1.2
Senorita	*Oxyjulis californica*	0	4	4	0.9
White seabass	*Atractoscion nobilis*	1	3	4	0.7
Bonefish	*Albula vulpes*	2	2	4	0.5
Unidentified larvae	unidentified Teleosti	4	0	4	0.5
Opaleye	*Girella nigricans*	0	3	3	0.7
Rockpool blenny	*Hypsoblennius gilberti*	0	3	3	0.2
Pacific sardine	*Sardinops sagax*	2	0	2	0.5
Pile perch	*Rhacochilus vacca*	0	2	2	0.5
Anchovy larva	unidentified Engraulidae	1	0	1	0.2
Chocolate pipefish	*Syngnathus euchrous*	0	1	1	0.2
Hornyhead turbot	*Pleuronichthys verticalis*	0	1	1	0.2
Longjaw mudsucker	*Gillichthys mirabilis*	0	1	1	0.2
Pacific barracuda	*Sphyraéna argentea*	1	0	1	0.2
Rock wrasse	*Halichoeres semicinctus*	0	1	1	0.2
Striped mullet	*Mugil cephalus*	1	0	1	0.2
White seaperch	*Phanerodon furcatus*	0	1	1	0.2

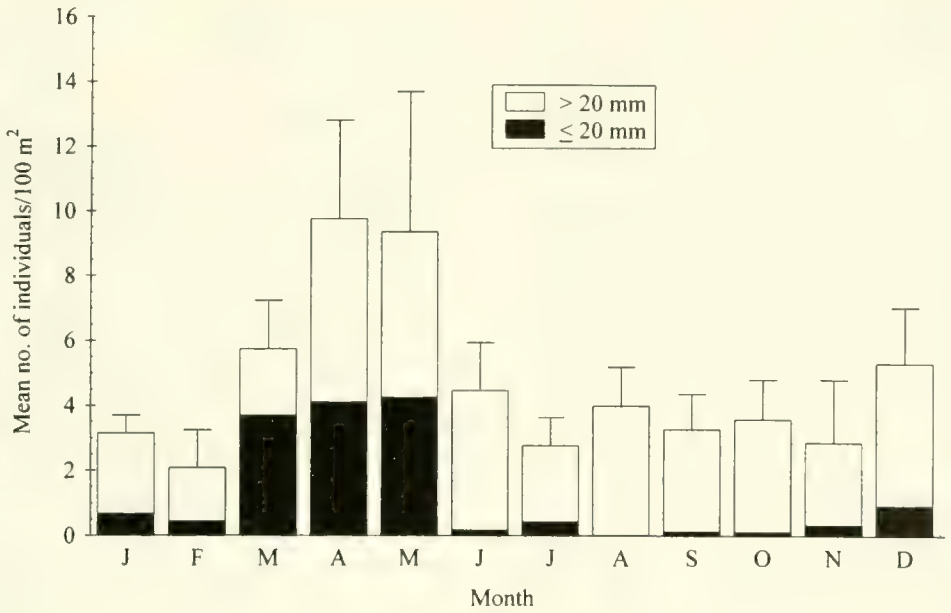

Figure 2

Mean number per 100 m^2 of newly settled (≤20 mm SL) and larger California halibut (*Paralichthys californicus*) captured by month in Alamitos Bay from May 1992 through November 1995 (n=435 tows). Error bars represent + one standard error for the total number of halibut per 100 m^2 captured by month.

halibut abundance decreased as distance from the bay mouth increased. Within unvegetated areas, California halibut were approximately 6 and 14 times more abundant at Bay Entrance than at Belmont Shore and Marine Stadium, respectively.

California halibut length ranged from 7 to 253 mm SL, but few were larger than 140 mm SL; no adults were captured. Lengths were similar among habitats and sites except that many more newly settled individuals were captured in unvegetated areas than in eelgrass beds, particularly at Bay Entrance (Fig. 4). The length-frequency distribution of California halibut in unvegetated habitat at Bay Entrance was significantly different from nearby eelgrass (P=0.007) and from Belmont Shore unvegetated area (P=0.001). No other length-frequency comparisons were significantly different (P>0.05).

Table 3

Results of Kruskal-Wallis test (KW) and Dunn multiple comparisons (D) of California halibut (*Paralichthys californicus*) abundance between habitats and among sites. df=degrees of freedom, H=Kruskal-Wallis statistic. BE=Bay Entrance, BS=Belmont Shore, MS=Marine Stadium, U=unvegetated habitat, and E=eelgrass (*Zostera marina*) habitat. *=significant at P<0.05.

Comparison	Test	df	Statistic	P-value
Habitat (U vs. E)				
BE	KW	1	H=55.58*	0.0001
BS	KW	1	H=16.03*	0.0001
MS	KW	1	H=5.80*	0.0161
Site (U)	KW	2	H=115.23*	0.0001
BE vs. BS	D		*	<0.05
BE vs. MS	D		*	<0.05
BS vs. MS	D			<0.05
Site (E)	KW	2	H=22.65*	0.0001
BE vs. BS	D		*	<0.05
BE vs. MS	D		*	<0.05
BS vs. MS	D			>0.05

Barred sand bass

We collected 225 barred sand bass from 12.4% of the tows (Table 2). The number of barred sand bass captured per tow ranged from 0 to 42 with a mean of 0.5 ± 0.14 SE. Newly recruited barred sand bass and most larger juveniles were captured from September through November (Fig. 5). Barred sand bass were captured almost exclusively (98.2%) in eelgrass beds and none were captured at Marine Stadium (Fig. 3B), leading to a significant interaction term in the two-way ANOVA (P=0.003). Because barred sand

bass were not captured at Marine Stadium and few were captured in unvegetated areas, only numbers within eelgrass beds at Bay Entrance and Belmont Shore were tested. Although approximately twice as many individuals were caught at Bay Entrance than at Belmont Shore, these results were not significantly different (P=0.68).

Lengths of barred sand bass ranged from 16 to 92 mm SL but most (66.2%) were ≤40 mm SL; no adults were captured. Average length at Bay Entrance (34.1 mm ±1.1 SE, n=156) was smaller than at Belmont Shore (43.5 mm ±1.4 SE, n=67), primarily due to the greater abundance of new recruits and small juveniles (21–30 mm SL) at Bay Entrance (Fig. 6).

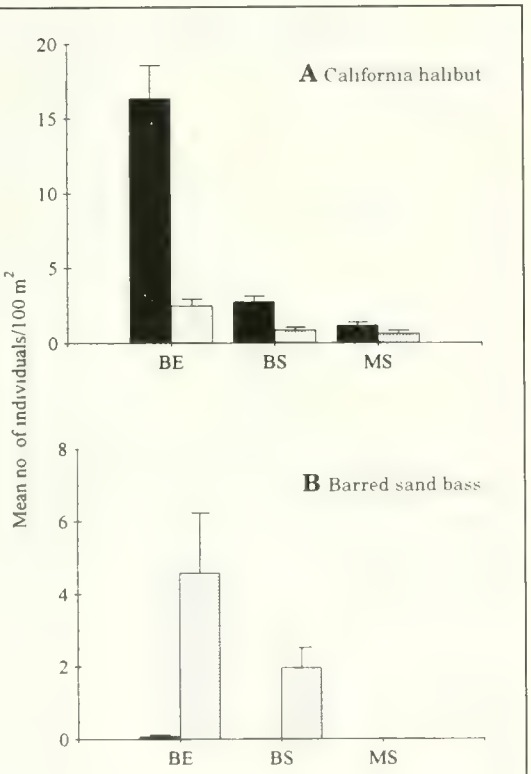

Figure 3

Mean number per 100 m^2 of (**A**) California halibut (*Paralichthys californicus*) and (**B**) barred sand bass (*Paralabrax nebulifer*) captured in unvegetated and eelgrass (*Zostera marina*) habitats at three sites in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. BE=Bay Entrance, BS=Belmont Shore, and MS=Marine Stadium. Number of tows in unvegetated habitats at BE, BS, and MS were 95, 61, and 95, respectively. Number of tows in eelgrass habitats at BE, BS, and MS were 60, 62, and 62, respectively. Error bars represent + one standard error.

Length-frequency distributions of barred sand bass at these two sites were significantly different (P= 0.0001).

Other species

Gobies were the most abundant group of fishes, accounting for 55.2% of the total (Table 2). This group comprised mostly arrow goby (*Clevelandia ios*), cheekspot goby (*Ilypnus gilberti*), and numerous goby larvae that were probably arrow goby and cheekspot goby. Bay pipefish (*Syngnathus leptorhynchus*), shiner perch (*Cymatogaster aggregata*), topsmelt (*Atherinops affinis*), and giant kelpfish (*Heterostichus rostratus*) were the other most abundant fishes, and along with gobies represented 87.9% of all individuals collected. These fishes, along with queenfish (*Seriphus politus*), diamond turbot (*Hypsopsetta guttulata*), spotted kelpfish (*Gibbonsia elegans*), shadow goby (*Quietula y-cauda*), Pacific staghorn sculpin (*Leptocottus armatus*), and bay blenny (*Hypsoblennius gentilis*), were considered "common fishes." The common fishes, along with California halibut and barred sand bass, accounted for 96.5% of the total number collected. Abundances for most of these fishes peaked from March through May or from June through August; most of these fishes were juveniles.

All of the common fishes were found in both habitats and at all sites; however the number of individuals varied considerably (Fig. 7). Only queenfish and Pacific staghorn sculpin had no significant interactions between habitat and site in the nonparametric two-factor ANOVA (P>0.05). Queenfish were significantly more abundant in unvegetated areas than in eelgrass beds (P=0.0003). No significant habitat differences were found for Pacific staghorn sculpin (P=0.41). Queenfish were significantly more abundant at Marine Stadium than at Belmont Shore (P<0.05), whereas Pacific staghorn sculpin were significantly more abundant at Belmont Shore than at Bay Entrance (P<0.05).

For 11 of the 13 common fishes, the nonparametric two-way ANOVA yielded significant interactions between habitat and site (P<0.05). Stratifying by site and comparing abundances between eelgrass and unvegetated areas, we found that bay pipefish, shiner perch, giant kelpfish, spotted kelpfish, shadow goby, and bay blenny were significantly more abundant in eelgrass than in unvegetated areas at all three sites (P<0.05). Cheekspot goby and diamond turbot were significantly more abundant in unvegetated areas than eelgrass at all three sites, whereas goby larvae and arrow goby were significantly more abundant in unvegetated areas at Belmont Shore (P<0.05).

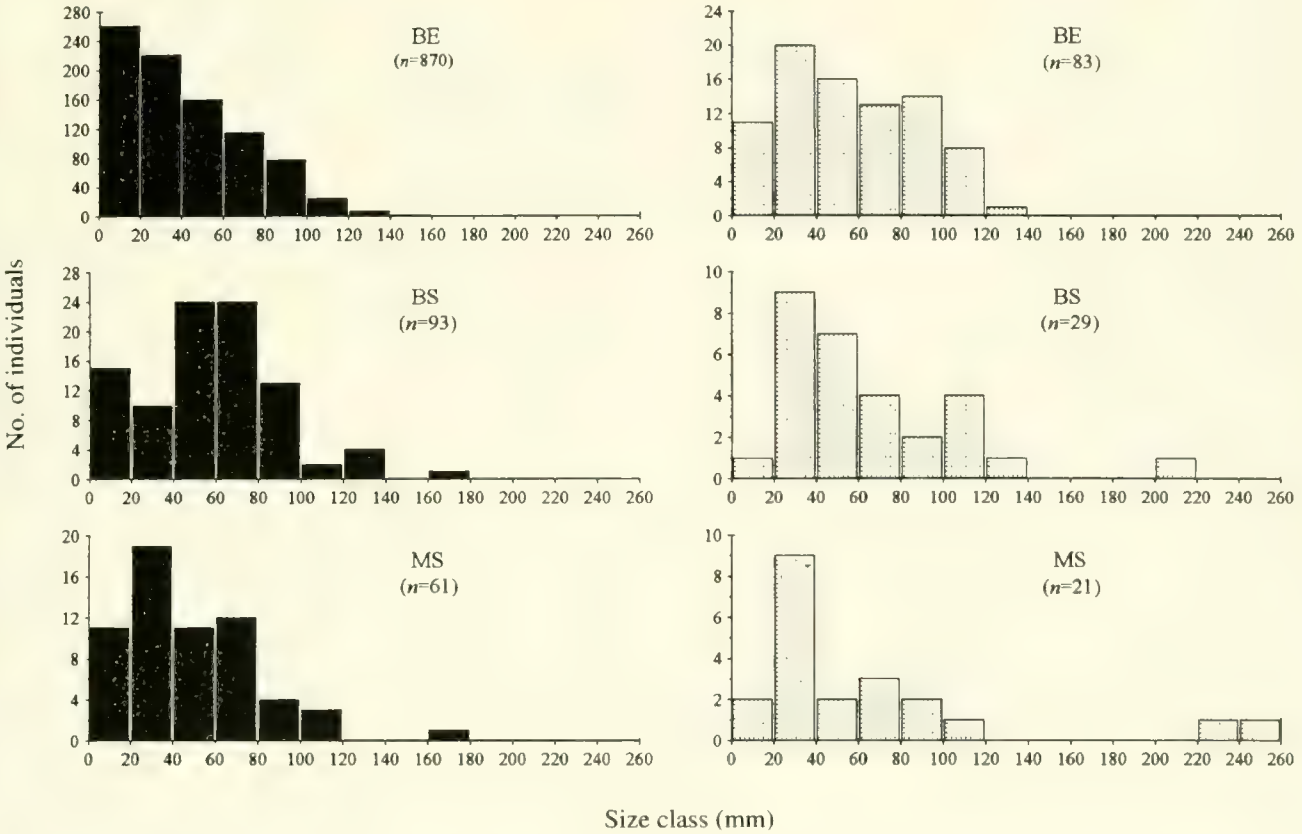

Figure 4

Length-frequency distributions of California halibut (*Paralichthys californicus*) captured in unvegetated and eelgrass (*Zostera marina*) habitats in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. See Figure 3 for further explanation.

Topsmelt showed a mixed pattern; they were significantly more abundant in eelgrass at Marine Stadium ($P<0.05$) but significantly more abundant in unvegetated area at Belmont Shore ($P<0.05$).

Stratifying by habitat and comparing abundances among sites, we found that most fishes were significantly more abundant at Marine Stadium or at Belmont Shore ($P<0.05$) (Table 4). Only shiner perch, giant kelpfish, and bay blenny had significantly more individuals at Bay Entrance than at one of the other two sites, but abundances at Bay Entrance were never significantly greater than at both of the other sites.

Discussion

California halibut and barred sand bass

Abundance of California halibut was habitat specific. California halibut was one of the few fishes whose abundance was much higher in unvegetated areas than in eelgrass beds. Although eelgrass blades may provide shelter from predation for some inhabitants (Heck and Thoman, 1981; Sogard and Olla, 1993), California halibut typically avoid detection by predators and prey by partially burying themselves in sediment (Haaker, 1975). Other flatfishes show substrate preferences (Tanda, 1990; Burke et al., 1991; Rogers, 1992), and California halibut ≤63 mm SL prefer bare sand over eelgrass in the laboratory (Drawbridge, 1990). Thus, sediments supporting eelgrass beds may not be preferable for settlement. It is also possible that eelgrass physically impedes halibut from settling there. If this were solely the case, then fewer halibut would be expected in eelgrass beds where distances between shoots were shorter (dense beds) than in beds where distances between shoots were greater (sparse beds). However, we found this not to be true; more halibut were found in a dense eelgrass bed (Bay Entrance) than in a sparse bed (Belmont Shore).

Barred sand bass abundance was also habitat specific; they were almost exclusively found in eelgrass

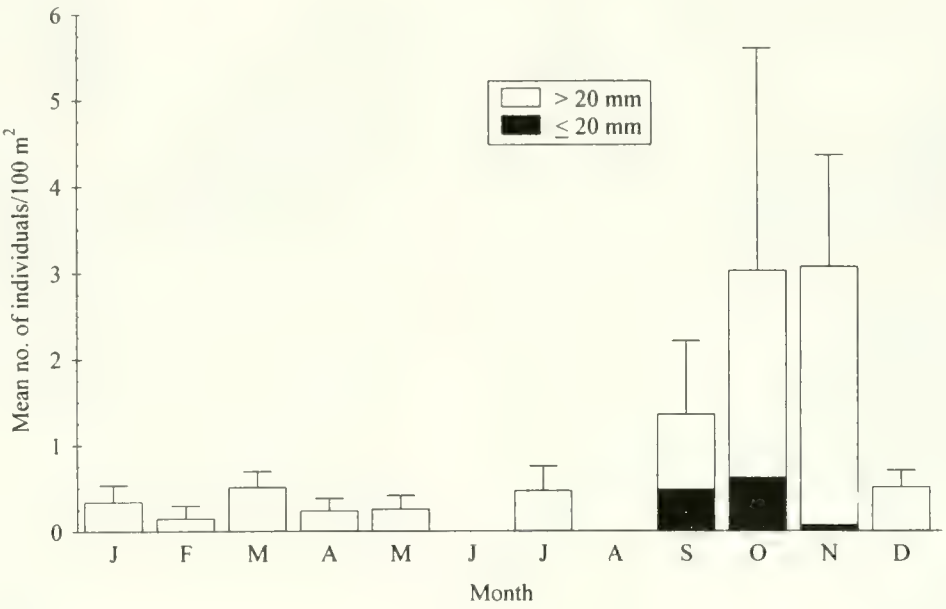

Figure 5

Mean number per 100 m^2 of newly recruited (≤20 mm SL) and larger barred sand bass (*Paralabrax nebulifer*) captured by month in Alamitos Bay from May 1992 through November 1995 (n=435 tows). Error bars represent + one standard error for the total number of barred sand bass per 100 m^2 captured by month.

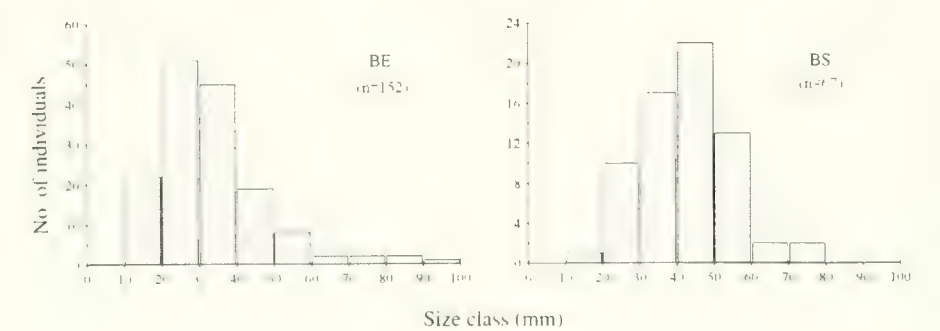

Figure 6

Length-frequency distributions of barred sand bass (*Paralabrax nebulifer*) captured in eelgrass (*Zostera marina*) habitat in Alamitos Bay from May 1992 through November 1995. See Figure 3 for further explanation

beds. Eelgrass beds may be productive foraging areas for them. Although the diet of newly recruited and small juvenile barred sand bass is not known, larger juvenile barred sand bass (123–239 mm SL) consume amphipods, shrimps, and other small crustaceans (Roberts et al., 1984). These items are often abundant in eelgrass beds, and this plentiful food supply may enable them to achieve faster growth rates, enabling them to achieve a size that is less vulnerable to predation more quickly (Levin et al., 1997). Additionally, eelgrass may offer shelter because most newly recruited and juvenile barred sand bass have been observed around eelgrass or other structure such as mussels, rocks, or debris during SCUBA surveys (senior author's unpubl. data). Larger juveniles and adults are mostly found over sandy bottoms and among rocks (Turner et al., 1969; Feder et al.,1974) and are scarce in eelgrass beds (senior author's unpubl. data).

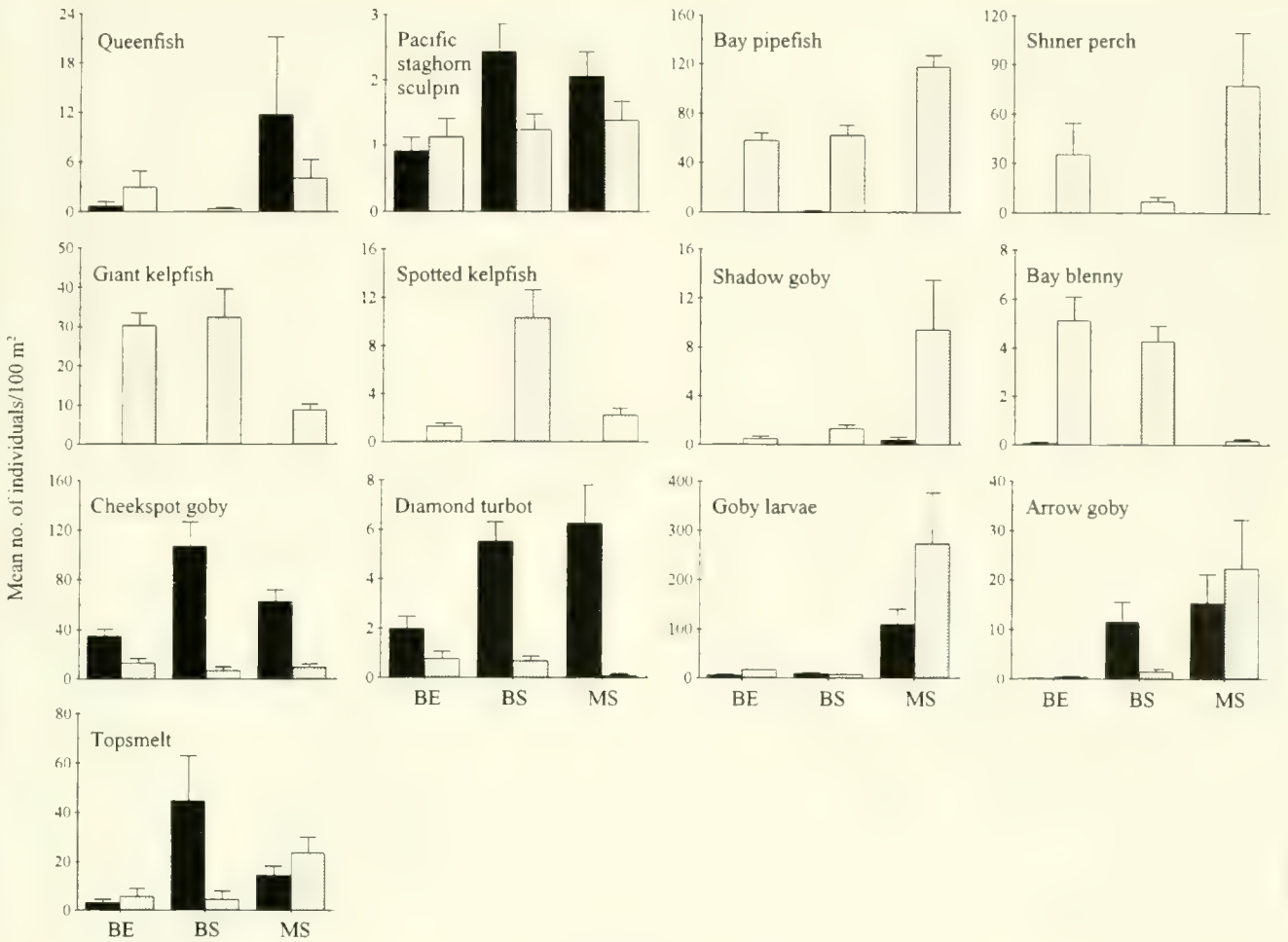

Figure 7

Mean number per 100 m^2 of the most abundant fishes (see text) captured in unvegetated and eelgrass (*Zostera marina*) habitats at three sites in Alamitos Bay from May 1992 through November 1995. Dark bars represent unvegetated habitats and stippled bars represent eelgrass habitats. See Figure 3 for further explanation.

The distribution patterns of California halibut and barred sand bass among sites were similar; abundances of individuals decreased with increasing distance from the bay mouth. These patterns in Alamitos Bay might be expected if abundances were related to larval supply because both species spawn outside the bay. Others have found that circulation patterns may limit dispersal of recruits to inner parts of an embayment (Sogard et al., 1987; Jenkins et al., 1996). However, this does not seem to be the case for Alamitos Bay because it is well circulated with a net inflow of water, and the distance between sites is relatively short. Instead, fewer halibut and barred sand bass may inhabit the inner parts of the bay because settlement and location of suitable habitat have occurred before reaching these areas. For California halibut, few larvae are found in embayments (White, 1977; Leithiser, 1981; Nordby, 1982; Yoklavich et al., 1992); the greatest densities of eggs and early larvae occur in nearshore waters with older larvae found less than 1 km from shore (Ahlstrom and Moser, 1975; Gruber et al., 1982; Barnett et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990). Most transforming halibut larvae are found on the open coast (Kramer, 1990, 1991a), and large numbers of halibut settle there and in embayments (Allen, 1988; Allen and Herbinson, 1990, 1991; Kramer, 1990, 1991a, 1991b). Those halibut that settle on the open coast move into embayments or die (Kramer, 1991a). Although it is not known where most barred sand bass recruitment occurs, spawning occurs in nearshore waters, and the planktonic larval phase is relatively short, lasting about one month (Butler et al., 1982). Therefore, if

Table 4

Results of Dunn multiple comparisons of fish abundance among sites. BE=Bay Entrance, BS=Belmont Shore, and MS=Marine Stadium. Comparisons among sites were done only for the habitat (eelgrass or unvegetated) where fishes were most abundant. * indicates which site showed a significantly greater abundance at $P<0.05$.

Common name	Scientific name	BE vs. BS	BE vs. MS	BS vs. MS
Eelgrass				
Bay pipefish	*Syngnathus leptorhynchus*		*MS	*MS
Shiner perch	*Cymatogaster aggregata*	*BE		*MS
Giant kelpfish	*Heterostichus rostratus*	*BS	*BE	*BS
Spotted kelpfish	*Gibbonsia elegans*	*BS		*BS
Shadow goby	*Quietula y-cauda*		*MS	
Bay blenny	*Hypsoblennius gentilis*		*BE	*BS
Goby larvae	Gobiidae		*MS	*MS
Unvegetated				
Cheekspot goby	*Ilypnus gilberti*	*BS	*MS	
Diamond turbot	*Hypsopsetta guttulata*	*BS	*MS	*MS
Arrow goby	*Clevelandia ios*	*BS	*MS	
Topsmelt	*Atherinops affinis*	*BS		

habitat is suitable, one would expect more newly settled California halibut and newly recruited barred sand bass at sites nearest the entrance because they are more likely to encounter these areas first. This might be especially true for embayments where the entrance is small, such as in Alamitos Bay, which could enhance chances of individuals encountering a shallow site nearest the mouth of the bay.

It is also possible that the distribution patterns we observed were due to active site selection. Diamond turbot, whose larvae also occur in nearshore waters (Barnett et al., 1984; Walker et al., 1987) and are thus exposed to the same hydrodynamic processes, were most abundant in the inner part of the bay and least abundant nearest the mouth of the bay. Kramer (1991b) also obtained opposite distribution patterns for juvenile California halibut and diamond turbot. Burke (1995) found that the distribution of two newly settled flounders that immigrated to an estuary were influenced by the availability of preferred prey types. Although we have no data on invertebrate prey distributions among sites, it is possible that California halibut and diamond turbot also select sites on the basis of availability of their preferred food items. Juvenile California halibut and diamond turbot have very different diets: small juvenile California halibut feed mainly on small crustaceans (Haaker, 1975; Plummer et al., 1983; Allèn, 1988; Drawbridge, 1990), whereas juvenile diamond turbot feed mainly on polychaetes (Lane, 1975). As halibut grow larger, they become more piscivorous and gobies become an increasingly important part of their diet (Allen, 1988; Drawbridge, 1990). This might explain why we found relatively larger halibut at Belmont Shore than at Bay Entrance because this area contained more arrow gobies and cheekspot gobies. Inhabiting an area with preferred food items might lead to accelerated growth rates, which may be an advantage for reducing size-selective predation. Sogard (1992) found that winter flounder (*Pleuronectes americanus*) and tautog (*Tautoga onitis*) were most abundant in estuarine areas that supported faster growth rates. However, we can not discount that larval supply may also be a factor because the spawning locations of diamond turbot are not known. Lane (1975) suggested that spawning takes place in or very near the outer harbor. This area would be much closer than where halibut spawn, and inner parts of the bay would be closer to eggs and larvae. In addition, laboratory experiments indicate that diamond turbot larvae are able to survive longer periods of starvation than halibut larvae (Gadomski and Petersen, 1988). This may enable diamond turbot larvae to remain in the water column longer and reach inner parts of the bay whereas halibut larvae must settle earlier.

Barred sand bass may also actively select sites within Alamitos Bay. However, the differences in physical characteristics of eelgrass among sites appeared not to affect the abundance of new recruits and juveniles. Although Bay Entrance had significantly more eelgrass shoots and longer blade lengths than Belmont Shore, barred sand bass abundances at the two sites were not significantly different. This lack of difference suggests that the effect of seagrass physical characteristics on fish abundance breaks down over larger spatial scales. However, if barred sand bass settle indiscriminately into the first eelgrass bed encountered, we would have expected significantly more individuals nearest the bay mouth. Sogard (1989)

found that initial settlement patterns for some fishes in seagrass beds were altered considerably by movement to other areas. Our results indicate that this may be also true for barred sand bass because significantly larger fish were found at Belmont Shore, indicating that movement to this site from the site nearest the entrance after initial settlement may have occurred. However, we are not able to resolve why barred sand bass were absent from the inner part of the bay.

Densities of newly settled and juvenile California halibut in our study were much greater than those reported by others using similar gear in other bays. Kramer (1990) obtained maximum monthly means for shoreline habitats in Agua Hedionda Lagoon of 3.7 newly settled California halibut per 100 m^2 for all stations combined and 9.2 per 100 m^2 for a single station. These densities are approximately 25% and 11%, respectively, of the values we obtained for Alamitos Bay. Our maximum monthly mean number of newly settled California halibut was approximately four times greater than that obtained for nearby Anaheim Bay in 1989 (Allen and Herbinson, 1990). Thus, our results support the conclusion by Allen and Herbinson (1990) that there is a great deal of annual variability in numbers of newly settled and juvenile California halibut within and among embayments in southern California.

Although the beam trawl may capture demersal fishes such as California halibut less effectively in eelgrass beds than in unvegetated areas, this seems an unlikely explanation for the great differences in habitat specific fish abundances that we observed. First, we collected large amounts of eelgrass blades (occasionally with attached rhizome) in many tows, and SCUBA observations indicated that the beam trawl maintained continuous contact with the substrate in both habitats. Second, staghorn sculpin, which rest on the substrate, and shadow goby, which often burrow in the sediment, were frequently captured in both habitats. Because we collected data only at low tides during daylight hours, we have no information on how sampling at different tide heights and times of the day would have affected our results. Diel differences in fish abundance can occur in southern California bays (Horn, 1980; Hoffman[4]); however, there are no data to suggest that these differences are related to habitats or locations within the bay.

Other species

Alamitos Bay was typical of other temperate bay-estuarine environments in having relatively few species account for a large proportion of the total number of individuals collected (reviewed in Allen and Horn, 1975; Horn, 1980; Allen, 1982; Onuf and Quammen, 1983; Allen and Herbinson, 1991; Hoffman[4]; MBC Applied Environmental Sciences[5]). Species composition and abundance were very similar to data collected using similar gear in Anaheim Bay and Agua Hedionda Lagoon (Allen and Herbinson, 1991; MBC Applied Environmental Sciences[5]). Our results, however, lacked high abundances of northern anchovy (*Engraulis mordax*), slough anchovy (*Anchoa delicatissima*), deepbody anchovy (*Anchoa compressa*), and California killifish (*Fundulus parvipinnis*) found by other studies in the inner part of Alamitos Bay and Newport Bay (Allen and Horn, 1975; Allen, 1982). Differences in sampling gear and location are probably responsible, but other factors may also play a role. As noted by Allen and Horn (1975), the abundance of northern anchovy may have been due to high periods of recruitment. Indeed, recruitment biomass of northern anchovy (age zero at 1 July) off southern California during their studies (1973 and 1979) was 2.6–3.1 times greater than during 1992–94 (Jacobson et al.[6])

For most species, greater abundances of individuals in either eelgrass or unvegetated areas suggested habitat preferences or differential mortality for these species in shallow water of Alamitos Bay. The large numbers of species and individuals in eelgrass beds indicated the importance of this habitat for many fishes, especially juveniles during spring and summer. Many of the fishes also differed in abundance across sites. More species were found near the bay mouth owing in part, to the occasional presence of more typical nearshore residents, but more individuals of several species were found farther inside the bay. However, the differences in eelgrass physical characteristics among sites did not appear to affect the abundances of most fishes. For example, abundances of bay blenny, bay pipefish, and shadow goby were not significantly different between Bay Entrance and Belmont Shore, although eelgrass density and blade lengths were significantly different between these sites. In addition, giant kelpfish and spotted kelpfish were most abundant at Belmont Shore, the site with the lowest eelgrass density and

[4] Hoffman, R. S. 1986. Fishery utilization of eelgrass (*Zostera marina*) beds and non-vegetated shallow water areas in San Diego Bay. National Marine Fisheries Service, Southwest Region, 501 W. Ocean Blvd, Suite 4200, Long Beach, CA, 90802. Admin. Rep. SWR-86-4, 29 p.

[5] MBC Applied Environmental Sciences. 1990. Distribution of juvenile California halibut (*Paralichthys californicus*) and other fishes in bay and coastal habitats of Los Angeles, Orange, and San Diego counties in 1989. MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627. Final Rep. 90-RD-09, 27 p.

[6] Jacobson, L. D., N. C. H. Lo, S. F. Herrick Jr., and T. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic fishery during 1994. Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, P. O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-95-11, 49 p.

shortest blade lengths. Only shiner perch abundance appeared related to eelgrass physical characteristics. This was not surprising because shiner perch are closely associated with the amount of eelgrass cover (Onuf and Quammen, 1983).

In conclusion, we found that for Alamitos Bay: 1) shallow unvegetated and eelgrass habitats were important for many fishes, especially juveniles, 2) juvenile California halibut and barred sand bass used different habitats; California halibut inhabited unvegetated areas and barred sand bass inhabited eelgrass beds, 3) habitats nearest the bay mouth were particularly important for juvenile California halibut and barred sand bass, whereas habitats farther inside the bay were more important for other fishes, 4) habitat and site selection for juvenile California halibut, barred sand bass, and most other fishes appeared unrelated to physical characteristics of eelgrass or abiotic factors, 5) habitat and site selection for juvenile California halibut and barred sand bass may be related to larval supply and to the first suitable habitat and site encountered, but may be modified subsequently by movement into other areas in search of preferred food items. A closer look at shallow unvegetated and eelgrass habitats in other bays in relation to California halibut and barred sand bass abundance is warranted. Protection of these habitats from elimination or even alteration may be important for the successful management of these species.

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Abstract.—A population model incorporating temporal and spatial detail revealed that the majority of eastern Georges Bank haddock, *Melanogrammus aeglefinus*, were found on the Canadian side of the Canada-U.S. boundary. During spring they were more widespread across the top of the bank and subsequently migrated eastward so that by fall almost all haddock were found in the deeper waters on the Canadian side. There is a return migration to the top of the bank during the winter. The seasonal distribution and migration of haddock has remained stable since 1985 and migration rates do not appear to be related to the observed range of abundance. The distribution pattern since 1985 appears similar to that observed between 1972 and 1984. In contrast, during 1963–71 haddock were more widespread throughout the area in both spring and fall. Abundance of haddock in the Georges Bank and Gulf of Maine area was exceptionally high in the earlier period, and haddock from the spawning component in the Great South Channel area may have accounted for a greater augmentation to the eastern Georges Bank population. In implementing strategies for managing this transboundary resource, scientists will need to evaluate the nature of haddock distributions in order, in turn, to evaluate the implications of their strategies.

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Movements of haddock, *Melanogrammus aeglefinus*, on eastern Georges Bank determined from a population model incorporating temporal and spatial detail

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The haddock, *Melanogrammus aeglefinus*, on Georges Bank have supported a commercial fishery since the early 1900s. Since 1977, with the extension of jurisdiction by coastal states, only Canada and the United States have conducted haddock fisheries on Georges Bank. In October 1984 the International Court of Justice (ICJ) established a maritime boundary between Canada and the United States in the Gulf of Maine area. Subsequently, fishing by Canada and the United States on Georges Bank has been restricted to these respective jurisdictions (Fig. 1). The new boundary line, referred to as the ICJ line in our study, lies over an established grid of statistical unit areas that has been used to summarize landings data since the 1930s. These areas have been based on, among other factors, considerations of biological stock structure (principally cod, *Gadus morhua*, and haddock), political boundaries, and practicalities of data collection (Halliday and Pinhorn, 1990). Aggregates of unit areas are used to determine the boundaries of fisheries "management units"—geographic areas defined for regulatory purposes.

Prior to establishment of the maritime boundary, regulation of the haddock fishery was based on a management unit encompassing all of subarea 5, although it was recognized that this unit included at least two major spawning concentrations (Walford, 1938; Bigelow and Schroeder, 1953). Historical evidence indicates that the most important spawning concentration was on the eastern part of Georges Bank whereas the spawning was variable among years over the Great South Channel and the southern part of the bank (Walford, 1938). Tagging studies and other biological data have shown that little mixing occurs between haddock on Georges Bank and those in surrounding areas, e.g. 4X (Fig. 1), which is situated north and east of Georges Bank (Schuck and Arnold, 1951; Grosslein, 1962; Clark et al., 1982). Tagging studies have also indicated limited east–west movement within subdivision 5Ze, which is the eastern portion of division 5Z and includes unit areas g, h, j, m, n, and o (Fig. 1), as only about 5% of returns from haddock tagged off Cape Cod were reported from areas east of 68°W and 95% of returns from haddock tagged on eastern Georges Bank were reported from areas east of 69°W (Grosslein, 1962). In 1990, Canada adopted unit areas 5Zj and 5Zm,

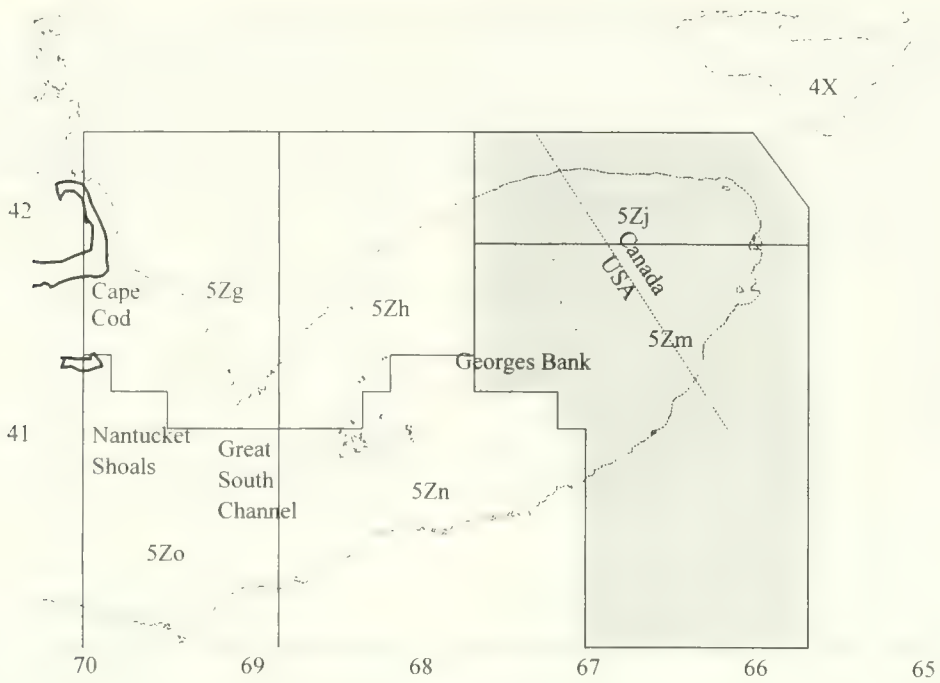

Figure 1

Fisheries statistical unit areas in NAFO subdivision 5Ze (includes 5Zg,h,j,m,n,o). The Canadian management unit for haddock comprises unit areas 5Zj and 5Zm (shaded).

eastern Georges Bank, as a management unit. Gavaris and Van Eeckhaute (1990) summarized the considerations on which the management unit boundaries are based. The ICJ line bisects this management unit and imposes additional complexity for resource management considerations in the absence of consistent practices by the two jurisdictions. A prerequisite to investigation of harvest strategies for the transboundary haddock resource is an understanding of haddock distribution and migration on eastern Georges Bank in relation to the ICJ line.

Earlier studies have described spatial distribution of Georges Bank haddock and patterns in relation to season, topography, time, and hydrographic conditions (Colton, 1955; Grosslein, 1962; Overholtz, 1985, 1987). Our study focuses on the relative distribution and net migration rates of haddock within the 5Zj,m Canadian management unit in relation to the ICJ line. Our objectives were to describe the relative abundance of haddock on the Canadian and U.S. sides of eastern Georges Bank since 1963 and to estimate rates of migration for haddock across the ICJ line since 1985 when fishery statistics first became available at a resolution sufficient to be summarized with respect to the ICJ line. These results are necessary for the evaluation of the effects of regulatory measures, whether unilateral or bilateral.

Methods

Relative abundance

Results from research vessel bottom trawl surveys were used to estimate haddock abundance on the Canadian and U.S. sides of the ICJ line on eastern Georges Bank and to subsequently derive ratios of abundance on the Canadian side to total 5Zj,m abundance. Annual surveys have been conducted by the U.S. National Marine Fisheries Service (NMFS) during the fall since 1963 and during the spring since 1968 and by the Canadian Department of Fisheries and Oceans (DFO) during the spring since 1986. Ratios of relative abundance were calculated to 1993 for the NMFS surveys and to 1994 for the DFO surveys, but survey data beyond those years were used to illustrate haddock distribution patterns as the data became available. All surveys used a stratified random design but the strata boundaries differed (Fig. 2). The strata boundaries for the DFO survey were modified to incorporate the ICJ line as a border in 1987. The results from the DFO survey in 1986, which used a different strata design, were not considered in our study owing to the complication that such a design would introduce and to the limited additional information that would result.

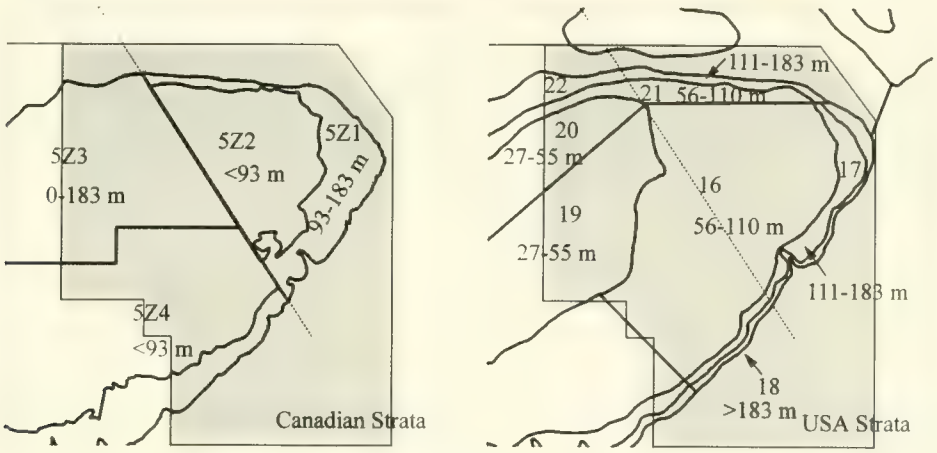

Figure 2

Strata for DFO and NMFS bottom trawl surveys with depth ranges. Several NMFS strata are bisected by the Canada-U.S. boundary line. Some strata for both countries are bisected by the 5Zj and 5Zm unit area boundaries.

The DFO surveys have been conducted by the RV *Alfred Needler* and for one year, by its sister ship, the RV *Wilfred Templeman*, with a Western IIA trawl. The NMFS surveys have been conducted by the RV *Albatross IV* and the RV *Delaware II* with a BMV door until 1984 and a polyvalent door subsequently. A further gear alteration occurred with the replacement of the standard Yankee 36 trawl by a modified Yankee 41 trawl during the spring surveys in 1973–81 (Hayes and Buxton[1]). Conversion factors to account for these differences were not considered in this study because the analysis involved only within-year comparisons. In the autumn of 1985, 1986, and 1988, both NMFS vessels made tows in the 5Zjm area but there was only one instance out of the three years, 1988, which would have resulted in slightly different ratios. The boat conversion factor was therefore not applied in our study.

Abundance of haddock on each side of the ICJ line was obtained by summing the estimates of abundance for the strata in the respective jurisdictions. This method can be applied directly to the Canadian side for the DFO survey results because the strata boundaries incorporate the ICJ line; however, the strata on the U.S. side, 5Z3 and 5Z4, are bisected by the 5Zj,m unit area lines (Fig. 2). Several strata in the NMFS surveys are bisected by the ICJ line or the 5Zj,m unit area lines, or by both (Fig. 2). We refer to the parts of the bisected strata as strata sections. Because the tow locations were selected at random, we computed the abundance of haddock in the strata sections in the same manner as was done for entire strata according to the method in Smith (1988). Total abundance on either side of the ICJ line was then obtained by summing the respective abundances from strata or strata sections, or from both. Abundance for each stratum or stratum section was obtained as the average catch per tow for tows within it multipied by the number of possible tow units within it, thereby weighting the average catch per stratum or stratum section by its area.

This approach could be applied in most instances; however, there were cases in the NMFS surveys where no tows were made in a stratum section (Tables 1 and 2). Missing observations were handled in three ways; by estimation using the multiplicative model, by assumption of a zero value, or by assigning the mean per tow obtained for the whole stratum. The multiplicative model (Gavaris, 1980) was the preferred method but it requires a ln transformation of the catch per tow from the surveys which precludes the use of "0" values in the model; therefore, for strata sections with low abundance, this model was inappropriate. The U.S. sections of strata 17 and 18 in both spring and fall surveys, the U.S. section of stratum 19 in the fall, and the Canadian section of stratum 18 in the spring had a predominance of "0" values, suggesting that it would be reasonable to assume a zero value for missing observations in those strata sections. Missing observations for U.S. stratum section 20 within 5Zj,m were assumed to be equal to the mean catch per tow obtained for the entire stratum that extends west of 5Zjm, and the age composition for the whole stratum was extrapolated to that portion lying within 5Zj,m. This procedure was first followed for the 1991 eastern Georges

[1] Hayes, D., and N. Buxton. 1992 Assessment of the Georges Bank haddock stock in 1991. Northeast Fisheries Science Center, Res. Doc. SAW 13/1. [Appendix to CRD-92-02.]

Table 1

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. side of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from fall NMFS bottom trawl surveys. When a stratum section was not sampled, as indicated by "( )", a multiplicative model was used to estimate abundance except for the U.S. side of strata 17, 18, and 19 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance that came from nonsampled strata or strata sections, or from both.

	Stratum												Total abundance		% from non sampled	
	16		17		18		19	20	21		22					
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1963	38,652	32,353	2148	0	(12,942)	0	30,950	4313	16,462	1942	(21,761)	3772	91,964	73,330	38	0
1964	31,485	45,050	667	62	358	0	45,126	8627	2095	(627)	(4535)	(555)	39,140	100,048	12	1
1965	11,434	7102	914	(0)	198	0	16,341	1849	2091	113	923	126	15,560	25,530	0	0
1966	7999	574	123	16	57	0	7034	3817	204	8	137	175	8521	11,624	0	0
1967	3543	344	131	0	102	5	1118	154	105	(50)	137	(45)	4018	1716	0	6
1968	4831	0	97	0	119	(0)	0	34	0	8	156	(16)	5203	58	0	27
1969	387	168	87	0	21	(0)	325	548	21	(12)	50	0	566	1052	0	1
1970	483	47	392	19	128	(0)	5005	0	242	8	125	(31)	1369	5111	0	1
1971	451	836	319	0	13	0	758	0	32	315	87	(39)	902	1948	0	2
1972	2313	3300	312	(0)	13	0	0	0	189	8	(375)	11	3202	3319	12	0
1973	11,515	230	735	0	19	0	0	0	347	(71)	(511)	(63)	13,128	363	4	37
1974	387	72	58	0	13	0	0	(0)	284	8	0	66	742	145	0	0
1975	6212	9756	602	(0)	64	0	108	5512	21	(92)	175	(81)	7073	15,549	0	1
1976	58,353	143	580	0	102	0	0	(0)	11,452	(236)	(1708)	55	72,195	435	2	54
1977	2641	42	421	0	(789)	0	22	0	13,809	129	1614	(162)	19,275	355	4	46
1978	6035	2374	4571	0	543	0	3809	126	821	0	271	55	12,240	6364	0	0
1979	7173	451	416	8	1465	0	22	9	491	(362)	6595	448	16,140	1299	0	28
1980	1643	112	3727	0	192	0	433	154	453	1200	1143	55	7157	1954	0	0
1981	3704	1865	1558	210	172	0	81	23	274	(180)	648	66	6356	2425	0	7
1982	591	36	1228	(0)	511	0	0	17	21	(29)	6	33	2358	115	0	25
1983	1369	947	735	(0)	192	0	0	0	158	(104)	(749)	77	3202	1127	23	9
1984	414	0	2133	(0)	141	0	0	0	116	(43)	(311)	55	3114	98	10	44
1985	5315	7231	588	(0)	324	0	0	0	568	(139)	25	(123)	6819	7493	0	3
1986	6845	0	892	(0)	358	0	0	0	2274	40	12	0	10,381	40	0	0
1987	81	179	271	(0)	115	0	135	103	316	0	312	0	1094	417	0	0
1988	2537	143	493	(0)	741	0	0	0	1179	(78)	362	0	5311	222	0	35
1989	852	47	1190	(0)	(311)	5	0	103	1379	16	573	16	4447	176	7	0
1990	564	915	1204	0	345	(0)	0	0	1165	(120)	170	(106)	3448	1141	0	20
1991	483	245	609	(0)	(124)	0	(0)	0	0	315	274	0	1491	560	8	0
1992	709	2869	1219	50	64	(0)	0	228	147	0	75	(39)	2214	3188	0	1
1993	1519	0	667	(0)	0	(0)	0	34	8041	(35)	162	(31)	10,390	99	0	66

Bank haddock assessment (Gavaris and Van Eeckhaute, 1991) and therefore the method used then was followed in our study. For all other missing observations that occurred in strata which did not have a predominance of zero values, a multiplicative model employing strata and years as factors influencing the mean catch per tow was used to derive predicted values:

$$\ln I_{s,y} = \ln I'_{s',y'} + \sum_{s} (\ln P_s) X_s + \sum_{y} (\ln P_y) X_y + \varepsilon_{s,y},$$

where s = stratum;
y = year;
I = survey catch/tow;
P = relative power for stratum or year;
X = dummy variables indicating the stratum and year of observation; and
ε = independent identically distributed normal error.

Strata sections 17u, 18c, and 18u in the spring and strata sections 17u, 18u, and 19 in the fall were not included in the multiplicative model analysis because of the prevalence of zeros in these strata sections.

Table 2

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring NMFS bottom trawl surveys. When a strata section was not sampled, as indicated by "()", a multiplicative model was used to estimate abundance except for stratum 18 and the U.S. side of stratum 17 which were assigned an abundance of "0" and stratum 20 where the mean for the whole stratum was used. The last two columns show the percentage of the total abundance which came from nonsampled strata or strata sections, or from both.

	Stratum															
	16		17		18		19	20	21		22		Total abundance		% from non sampled	
Year	Can.	U.S.	Can.	U.S.	Can.	U.S.	U.S.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.	Can.	U.S.
1968	3318	1506	595	(0)	43	0	1515	274	32	(55)	(200)	77	4186	3427	5	2
1969	2164	1119	445	0	0	0	397	34	11	(25)	87	(21)	2707	1596	0	3
1970	713	7221	218	0	0	0	252	(21)	21	(26)	75	(21)	1027	7540	0	1
1971	139	430	194	0	0	5	271	0	14	73	374	(19)	720	797	0	2
1972	1002	215	310	0	0	0	144	0	91	1534	0	(20)	1403	1913	0	1
1973	2462	1052	443	(0)	0	0	685	46	21	186	1322	0	4248	1968	0	0
1974	9582	0	116	0	4	0	2841	0	416	(19)	(70)	0	10,189	2860	1	1
1975	4134	538	65	(0)	0	(0)	577	0	42	16	12	(17)	4254	1148	0	2
1976	3818	1052	629	(0)	0	(0)	406	(154)	358	16	(128)	0	4933	1628	3	9
1977	3221	502	48	0	0	0	681	1061	13,115	16	0	5	16,384	2266	0	0
1978	5738	2905	48	8	6	0	606	0	4652	(60)	33	(50)	10,479	3629	0	3
1979	7043	6743	319	23	0	(0)	401	(28)	253	0	594	87	8209	7284	0	0
1980	6120	27,212	254	54	6	(0)	24,863	(1124)	3694	0	112	(114)	10,187	53,367	0	2
1981	14,387	8704	638	3	(0)	(0)	6125	2659	1905	(246)	87	230	17,017	17,967	0	1
1982	5411	3945	416	233	6	0	397	251	1179	(113)	898	22	7910	4962	0	2
1983	1933	538	735	39	0	0	0	171	(1119)	16	87	109	3874	874	29	0
1984	2623	1255	305	(0)	0	0	433	17	105	8	37	33	3071	1746	0	0
1985	9133	574	252	31	38	0	108	0	1937	(50)	87	(41)	11,447	804	0	11
1986	6313	1521	29	0	0	0	433	0	1305	4	0	(18)	7647	1975	0	1
1987	5991	115	136	0	6	0	0	1872	126	(11)	25	(9)	6284	2007	0	1
1988	1417	1894	15	0	0	(0)	54	0	284	0	0	0	1716	1948	0	0
1989	4168	5022	392	93	153	(0)	27	0	1631	0	798	(40)	7142	5182	0	1
1990	4268	9756	44	0	(0)	(0)	0	0	1291	16	12	(23)	5615	9795	0	0
1991	9341	2254	48	(0)	0	(0)	0	0	74	0	0	0	9463	2254	0	0
1992	966	369	165	(0)	0	(0)	65	11	379	(10)	0	(8)	1510	464	0	4
1993	2791	841	551	(0)	0	(0)	0	0	365	(30)	237	(25)	3944	896	0	6

Treatment of missing observations is summarized in Table 3.

The multiplicative model requires a ln transformation of the catch per tow from the surveys. This necessitated some treatment of remaining "0" values in the data. To reduce the influence of "0" values, the strata means rather than individual tow data were used because there are frequent occurrences of "0" catch in the individual tow data. Consequently, a test for the significance of interaction between years and strata was not possible. Because a logarithmic transformation of the mean catch per tow is required, a constant less than the minimum catch was added to "0" values. To examine the impact of adding a constant to the zero observations, analyses using three different constants, 0.1, 0.01, and 0.001, were considered. It was found that smaller constants exerted a greater influence on the model's output as seen by increases in Cook's D statistic (Cook, 1977). Moreover, the frequency distribution of the residuals showed greater departure from a normal distribution when 0.01 was added and particularly when 0.001 was added, displaying a marked skew toward negative values. Consequently, 0.1 was added to zero values for multiplicative model computations. The smallest observed value greater than "0" was 0.2.

For each survey, an age-length key combining all strata on eastern Georges Bank was applied to the length composition in each stratum or stratum section to derive the age structure. The age structures to which the estimated mean number per tow for missing values were applied were taken from the

Table 3

Treatment of missing observations in the NMFS spring and fall surveys to estimate abundance on the U.S. side and the Canadian side of unit areas 5Zj and 5Zm. c = Canadian side of stratum; u = U.S. side of stratum; *M* and **M** = used in multiplicative model; **M** = missing observations estimated from multiplicative model; 5Z = 5Z stratum mean used to fill in missing observations; 0 = missing observations assigned a value of 0.

Stratum	Spring	Fall
16c	*M*	*M*
16u	*M*	*M*
17c	*M*	*M*
17u	0	0
18c	0	**M**
18u	0	0
19	*M*	0
20	5Z	5Z
21c	**M**	**M**
21u	**M**	**M**
22c	**M**	**M**
22u	**M**	**M**

adjacent stratum section of the same stratum. When both strata sections of a stratum had missing observations, the age composition from an adjacent stratum was used. Haddock abundance at age on the Canadian and U.S. sides of the ICJ line were obtained by applying the age compositions of strata and strata sections to their respective total abundance and then summing the results within each jurisdiction. A ratio of relative abundance for the Canadian side was calculated by dividing the estimate on the Canadian side by the sum of the estimates on Canadian and U.S. sides.

Instantaneous rates of net migration

The availability of fisheries statistics, since 1985, at a resolution sufficient to be summarized with respect to the ICJ line, in conjunction with the relative abundance information described above, made it possible to derive estimates of net migration rates. Catch-at-age by quarter which was required for this analysis is reported in Gavaris and Van Eeckhaute (1997).

Net migration rates were estimated by using a model that follows from one originally proposed by Beverton and Holt (1957). Terminal population abundance for each cohort at the beginning of 1994 for the 1986 to 1993 year classes and at age 8 for the 1968 to 1985 year classes was taken from Gavaris and Van Eeckhaute (1994). Population abundance in all of 5Zj,m at time y, expressed in units of years, e.g. 1991.75, for ages 1–8, a, was calculated by using virtual population analysis with a three-month time period, i.e. t=0.25, according to the following algorithm. The annual instantaneous natural mortality rate, M, was assumed constant and equal to 0.2. In all equations N refers to numbers of fish and, if preceded by a subscript letter, indicates the source of the loss so that ${}_{F}N$ is the number dying from fishing, ${}_{M}N$ is the number dying from natural mortality, and ${}_{E}N$ is the number lost or gained from migration. If not preceded by a subscript, N refers to population abundance. The method assumes an exponential decay model:

$$N_{y,a} = N_{y+t,a+t} e^{(F_{y,a}+M)t},$$

where the fishing mortality, $F_{y,a}$, for ages 1 to 7 is obtained by solving the catch equation using a Newton-Raphson algorithm with the three-month commercial catch-at-age data, ${}_{F}N_{y,a}$.

$$N_{y,a} = \frac{{}_{F}N_{y,a}(F_{y,a}+M)t}{F_{y,a}t\left(1-e^{-(F_{y,a}+M)t}\right)}.$$

The total number of fish dying due to natural mortality in each quarterly period, y, was obtained by applying the quarterly rate of natural mortality to the average population abundance during the period:

$${}_{M}N_{y,a} = Mt\overline{N},$$

where $\overline{N}$, the average population abundance during the period, is defined as

$$\overline{N}_{y,a} = \frac{N_{y,a}\left(1-e^{-(F_{y,a}+M)t}\right)}{(F_{y,a}+M)t}.$$

DFO surveys were conducted between 10 February and 19 March, whereas NMFS spring surveys were conducted from 23 March to 26 April. The NMFS fall surveys were conducted between 3 October and 25 October. The distributions of haddock obtained from the spring and fall survey results were considered to be representative of 1 April and 1 October, respectively. For each year, six-month net migration rates were calculated for the spring–summer period (1 April–30 September) and the fall–winter period (1 October–31 March).

Since proportions of haddock on the Canadian side of the ICJ line, as indicated from DFO and NMFS survey results, were available for only two points in time, spring and fall, subsequent calculations were done on a half-year basis to coincide with the survey

timing. The 5Zj,m population numbers at the beginning of quarters 2 and 4 as obtained from the quarterly VPA were used. Numbers of haddock dying from natural mortality and from fishing were summed for quarters 2 and 3 to give 1 April numbers and for quarters 4 and 1 to give 1 October numbers. The proportions of haddock at ages 1 to 8 on the Canadian side of the ICJ line were averaged for the two spring surveys for 1987 to 1993. These were then combined with the 1985 and 1986 proportions from the NMFS spring survey and, along with the NMFS fall proportions, were applied to the 5Zj,m population abundance at the beginning of quarters 2 and 4 to obtain population abundance on the Canadian side:

$$N_{Can,y,a} = N_{y,a} R_{Can,y,a},$$

where $R_{Can,y,a}$ = the proportion occurring on the Canadian side.

The number of fish dying from natural mortality on the Canadian side of the ICJ line was assumed proportional to the fraction of the population occupying the Canadian side on average during the period:

$${}_M N_{Can,y,a} = \frac{{}_M N_{y,a} \overline{N}_{Can,y,a}}{(\overline{N}_{Can,y,a} + \overline{N}_{USA,y,a})},$$

where $\overline{N}_{Can,y,a}$ and $\overline{N}_{USA,y,a}$ = the average population abundances on the Canadian and USA sides, respectively, during the period.

The net number of fish migrating from the Canadian side to the U.S. side of the ICJ line was obtained by subtracting the number of fish caught by the Canadian fishery at age, $F^{N}_{Can,y,a}$, and the number of fish dying from natural mortality on the Canadian side from the difference between population abundance on the Canadian side at the beginning of the two six month periods:

$${}_E N_{y,a} = N_{Can,y,a} - N_{Can,y+t,a+t} - {}_F N_{Can,y,a} - {}_M N_{Can,y,a}$$

Instantaneous rates of migration were calculated in relation to the average abundance in 5Zj,m as follows:

$$E_{y,a} = \frac{{}_E N_{y,a}(Z_{y,a})}{N_{y,a}\left(1 - e^{-(Z_{y,a})}\right)},$$

where the total mortality

$$Z_{y,a} = -\ln \frac{N_{y+t,a+t}}{N_{y,a}}.$$

By convention, ${}_E N_{y,a}$ and $E_{y,a}$ is positive when the net direction of migration is towards the U.S. side and negative when it is towards the Canadian side.

Results

Ratios of relative abundance

Although the ICJ line was not established until October 1984, to provide a historical perspective of haddock relative abundance with respect to the line, we make reference to Canadian and U.S. sides of eastern Georges Bank for all surveys conducted since 1963. Because relative abundances of older haddock, greater than age 8, are difficult to interpret because of the small numbers caught, an aggregated age grouping of 9+ was used.

Fall season The multiplicative model accounted for about half of the total variation in catch per tow (multiple R^2=0.47). The stratum influence with an F-value of 7.245 and P<0.001 accounted for most of the variation, but the year effect also accounted for some with an F-value of 3.247 and P<0.001. The frequency distribution of residuals approximated a normal distribution. The strata coefficients from the multiplicative model give an indication of the relative abundances between strata sections, i.e. the higher the value, the higher the abundance. For those strata sections that were used in the model, the shading in Figure 3 was scaled to the magnitude of the strata coefficients. All Canadian sections of strata had higher coefficients than the corresponding U.S. sections. The four sections on the U.S. side that were not used in the model were dominated by zero catch per tow. Canadian strata sections having depth zones of 56 to 183 m exhibited the highest coefficients. The model results indicate that the strata on the Canadian side had higher abundance than those on the U.S. side.

For each stratum the abundances by stratum or stratum section are contained in Table 1. The dominant strata were 16c, 16u, and 17c. Abundance in 19u and 20u used to be quite high but in recent times almost no haddock have been caught there. In contrast, 17c has shown an increase in its relative abundance in recent years in comparison to early catches, although that abundance since the 1960s has dropped substantially. Total fall abundance showed that more haddock were caught on the U.S. side during the 1960s and early 1970s, after which haddock became more abundant on the Canadian side. Numbers estimated by the multiplicative model accounted for a significant amount of the abundance on the U.S. side

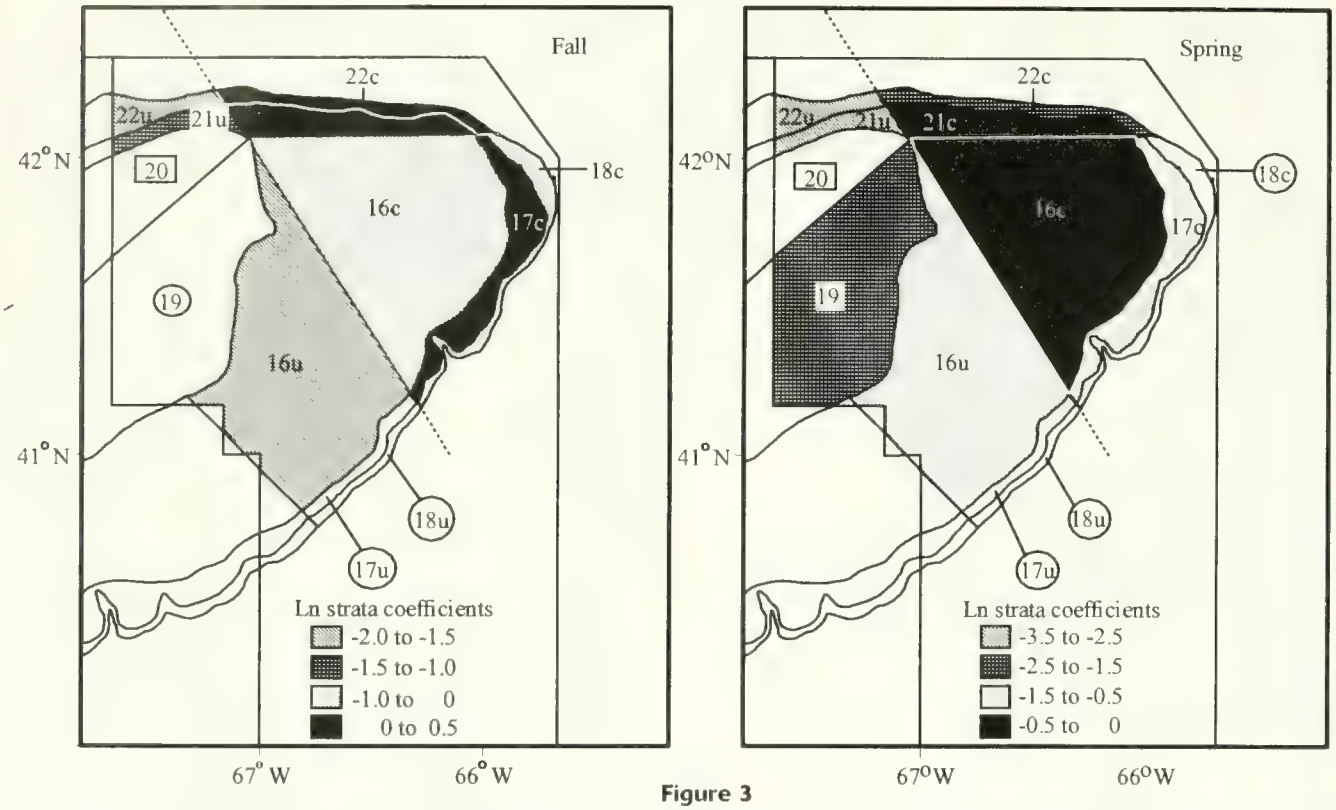

Figure 3

The relative abundances between strata as characterized by the ln strata coefficients from the multiplicative model for the NMFS fall and spring surveys. Strata which have a circle ( ) around them, e.g. 17u , were not used in the multiplicative model and missing observations were given a value of "0." Stratum 20 was also not used in the model because the 5Z stratum means were used for missing observations. Strata depth zones are as follows: 19 and 20, 27–55 m; 16 and 21, 56–110 m; 17 and 22, 111–183 m; 18, >183 m.

in several years but, in those years, the total abundance on the U.S. side was usually small. For the Canadian side, in most instances, very little of the abundance was estimated from the multiplicative model.

An examination of the fall ratios of relative abundance, (Fig. 4), revealed two distribution patterns in haddock age 1 and older. Between 1963 and 1972, haddock were highly variable in their relative abundance and were found throughout the bank. After 1971, the majority of haddock ages 1 and older were found on the Canadian side as indicated by the predominance of ratios ≥0.75. The ratios of relative abundance indicated that age-0 haddock were very variable throughout 1963–93 and were often more abundant on the U.S. side.

Friedman's nonparametric test revealed that the ratios for ages 1–9+ during the period 1972–93 were similar but the ratios for age 0 differed from these. During the period 1963–71, the ratios for all ages, 0–9+, did not show persistent patterns (Table 4).

We conclude then that the relative abundance of age-0 haddock across the ICJ line is different from that for ages 1–9+ but only during the period 1972–93. Therefore, for further analysis of time trends, ages 1–9+ were combined (Fig. 5). From 1963 to 1971 haddock of ages 1+ were distributed throughout 5Zj,m but were generally found in greater numbers on the U.S. side. Since 1972, however, very few haddock at these ages have been found on the U.S. side. Between 1963 and 1971, there was one anomolously high value, 1968 with a ratio of 0.99, but all other ratios were lower than any of the values after 1971. In contrast to ages 1+, the ratios of relative abundance of age-0 haddock were very variable and indicated a less patterned distribution, being distributed throughout 5Zj,m. All except one of the stronger year classes, 1972, 1975, 1978, 1983, 1985, 1987, and 1992, with relative abundance ratios at age 0 of 0.34, 0.28, 0.47, 0.62, 0.40, 0.21, and 0.08, respectively, were more abundant on the U.S. side. Interestingly, the weak year classes that followed these (1973, 1976, 1979, 1984, 1986, 1988, and 1993) were found in greater abundance on the Canadian side with ratios of 0.85, 0.85, 0.64, 1.0, 1.0, 1.0, and 0.93, respectively. A likely mechanism has not been determined.

The distribution of age-1+ haddock determined by using the catch-per-tow data from the NMFS fall survey, pooled over 1985–95, are shown in Figure 6. As

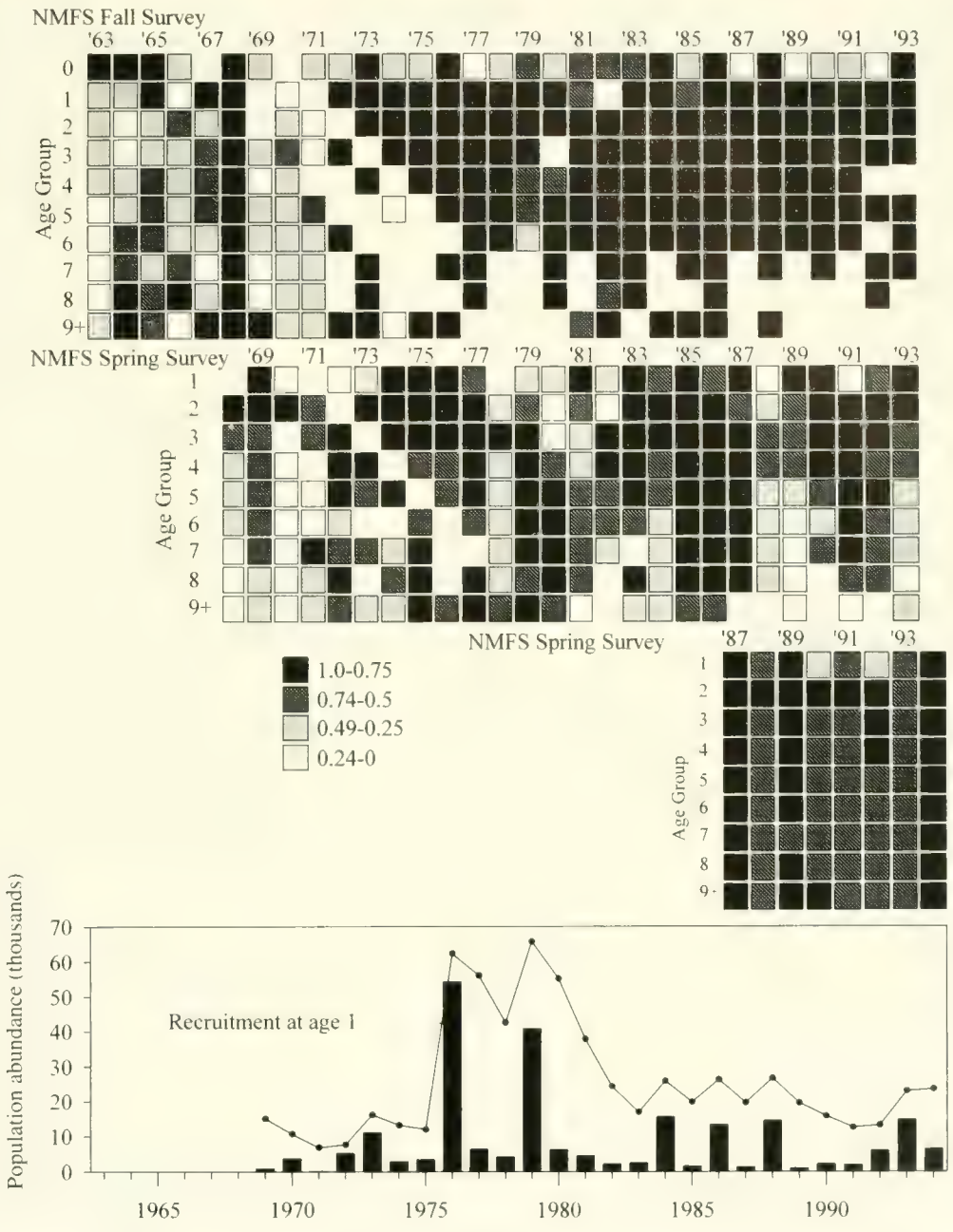

Figure 4

Ratios of relative abundance for haddock on eastern Georges Bank aggregated into four categories from the DFO and NMFS surveys and (below) population abundance and recruitment at age 1 in 5Zj,m as estimated by sequential population analysis by Gavaris and Van Eeckhaute (1995).

noted from the analyses of ratios of relative abundance, in recent times few haddock have been found on the U.S. side during the fall. For comparison purposes the 1963–71 distribution determined by using NMFS fall survey data are also shown. It is evident that the 1963–71 distribution pattern is markedly different from the 1985–95 patterns. The wide spread abundance observed west of the ICJ line in the 1963–71 period is no longer present in recent times and the aggregations on the northeast peak that were apparent from 1985 to 1995 were not evident in the earlier period.

Spring season As with the fall results, the multiplicative model accounted for about half of the total

Table 4

Probability estimates of Freidmans's nonparametric test for randomness within ages from the National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) survey ratios of relative abundance for two age groupings.

Age groups	Years	*F*-value	Degrees of freedom	Probability of test criterion
NMFS fall sSurvey				
0–9+	1963–71	8.424	9	$0.5 > P > 0.25$
0–9+	1972–93	25.185	9	$0.005 > P > 0.001$
1–9+	1972–93	0.8	8	$P > 0.999$
NMFS spring survey				
1–9+	1968–93	28.292	8	$0.001 > P$
DFO spring survey				
1–9+	1987–94	6.058	8	$0.75 > P > 0.5$

variation in catch per tow (multiple R^2=0.41). The stratum influence accounted for most of the variation with an *F*-value of 8.389 and $P<0.001$ but the year effect was not as strong for the spring survey as it was for fall (*F*-value of 1.647, $0.1<P<0.2$). The frequency distribution of residuals approximated a normal distribution, although not as well as those of the fall survey. An outlier from stratum 21u in 1972 influenced the model's estimates of abundances for that stratum; estimates were 60% greater than they would have been had this value been excluded from the analysis. A higher proportion of haddock on the Canadian side would have resulted if this value had been excluded. This stratum, however, does not contribute substantially to the overall abundance; therefore its impact was not studied further. The relative abundances between strata as characterized by the strata coefficients from the multiplicative model are shown in Figure 3. Two Canadian strata sections, 21c and 16c, which have a depth range from 56 to 110 m, had the highest coefficients. Three strata sections with a high number of zero values, 17u, 18c and 18u, were not used in the model.

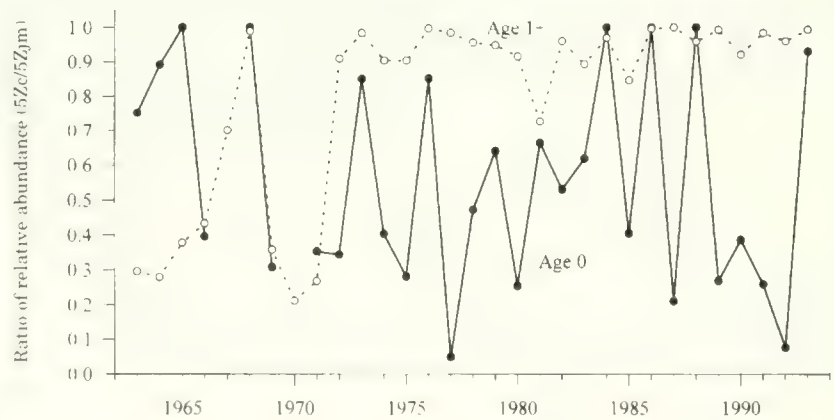

Figure 5

The distribution of haddock across the ICJ line in 5Zjm during the fall as indicated by the ratios of relative abundance from the NMFS fall survey.

The stratum and stratum section abundances from NMFS spring surveys are given in Table 2. Stratum section 16c, and 16u (secondarily), were again the highest contributors to total abundance. The relative contribution of stratum section 21c increased after 1976, whereas the contribution from stratum section 17c remained stable over time. As in fall, 19u in spring also declined in relative abundance from earlier times; very few haddock were caught there after 1981. The highest numbers in 19u were caught during 1980 and 1981. Haddock were virtually absent from 18c in spring but in the fall there were almost always some to be found there. Total abundance on the Canadian side was augmented by estimated numbers only four times, whereas most years were augmented for the U.S. side. The contribution made by these values to abundance on the U.S. side, however, was negligible.

Abundances by stratum for the DFO spring survey are given in Table 5. Haddock were always more abundant on the Canadian side than on the U.S. side; the Canadian side had 61–99% of the abundance in 5Zjm. Except for two occasions, haddock were more abundant in the shallower 5Z2 stratum than in the deeper 5Z1 stratum. Stratum 5Z2 and 5Z4 have the

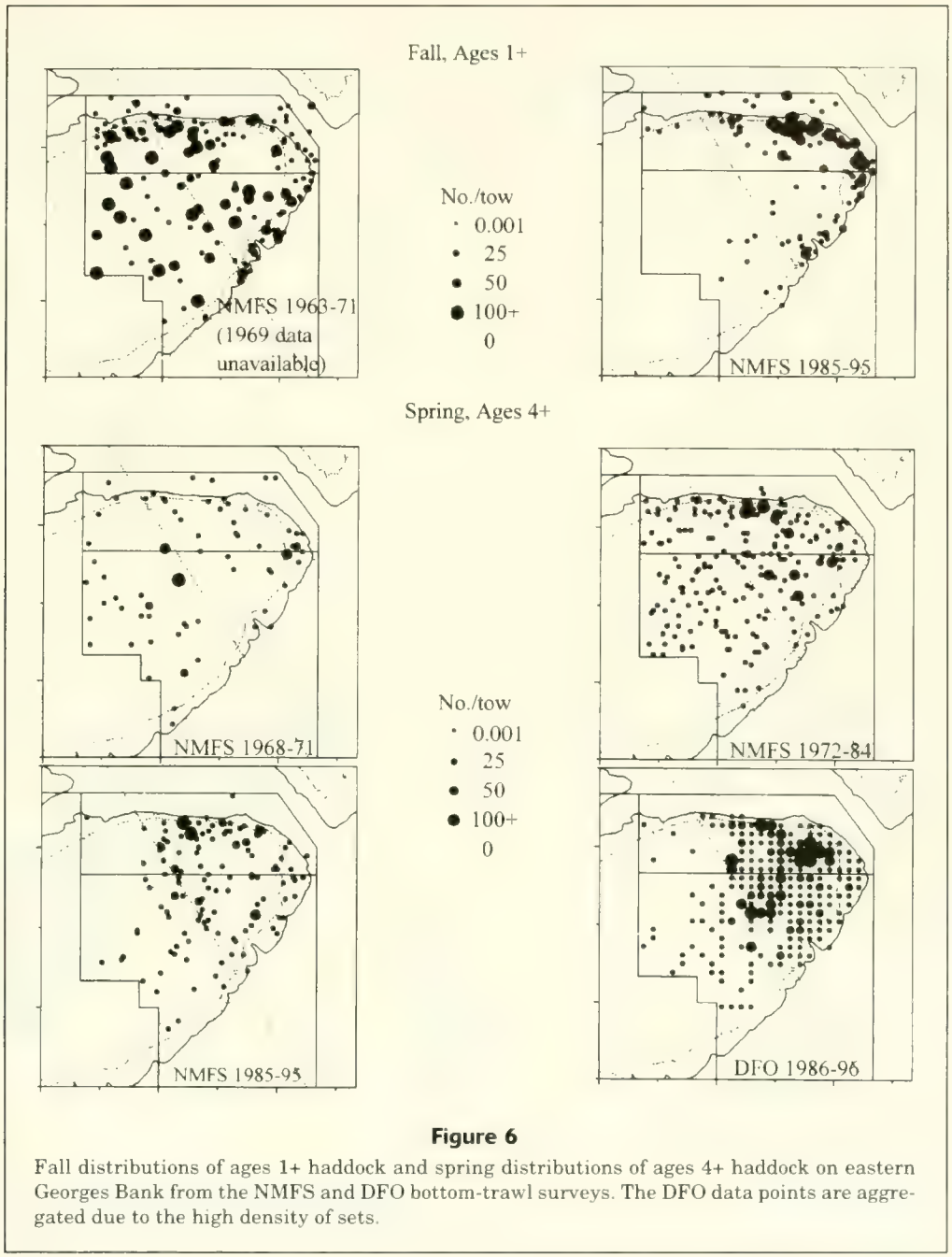

Figure 6

Fall distributions of ages 1+ haddock and spring distributions of ages 4+ haddock on eastern Georges Bank from the NMFS and DFO bottom-trawl surveys. The DFO data points are aggregated due to the high density of sets.

same depth range but, except for 1993, haddock were much more abundant in 5Z2.

The ratio of relative abundance trends from both the NMFS spring survey and the DFO spring survey indicated that haddock abundance is generally greater on the Canadian side of the ICJ line, though not as high as during the fall (Fig. 4). There was no obvious pattern by age in the ratios of abundance. The results of Friedman's test confirmed that there was not a significant age effect in the DFO spring survey but indicated that there were significant differences by age in the NMFS survey (Table 4). There was a tendency for lower ratios as age increases but the relationship was very weak (r^2=0.083 for ages 4–9+). Similarities in ratios of relative abundance among ages were examined with a correlation test of arcsine-transformed NMFS survey ratios. This revealed that age 1 did not correlate with any other ages (r<0.5), ages 2 and 3 showed some correlation with adjacent age classes, and ages 4–8 were highly correlated (r>0.5; Fig. 7). The ratios were plotted as three groups in Figure 8. For ages 4–8, there was

Table 5

Estimated abundance (numbers in thousands) of haddock by stratum on the Canadian and U.S. sides of the ICJ line in unit areas 5Zj and 5Zm (eastern Georges Bank) from spring Canadian Department of Fisheries and Oceans bottom trawl surveys.

	Canadian side		U.S. side		Total abundance	
Year	5Z1	5Z2	5Z3	5Z4	Canadian side	U.S. side
1987	3794	7162	103	40	10,956	143
1988	1398	12,444	5344	483	13,842	5827
1989	1874	9117	279	120	10,991	399
1990	4038	9903	1814	4214	13,941	6028
1991	2243	7961	3674	2429	10,204	6103
1992	4694	5540	2508	1507	10,234	4015
1993	2946	1879	37	2988	4825	3025
1994	15,424	11,091	167	180	26,515	347

more variability in the ratios from year to year than in the fall survey, but high values predominated except from the 1968–71 period when the ratios were lower. Ratios for age 1 were variable with no obvious tendency but most ages 2 and 3 ratios were greater than 0.5. The short length of the DFO survey series precluded investigation of this feature for these data.

The effect of total 5Zj,m abundance on the spring ratios of relative abundance was examined for this period because the greatest amount of dispersion onto the bank occurs during spring. This was evaluated by plotting the NMFS spring survey ratios of relative abundance against the beginning of year population numbers aggregated into three age groupings: age 1, ages 2 and 3, and ages 4–8. Population numbers were obtained from the 1995 eastern Georges Bank haddock assessment (Gavaris and Van Eeckhaute, 1995). No relation between abundance and ratios of relative abundance was apparent. The DFO time series was not investigated for this effect because of its short time span.

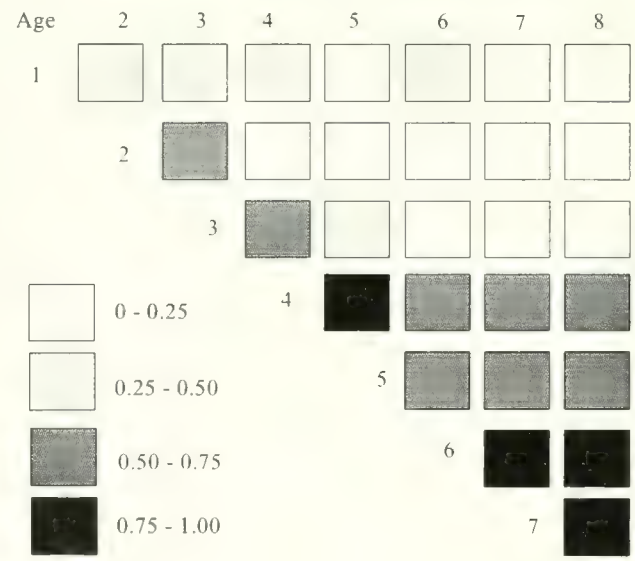

Figure 7

Age by age correlation of haddock ratios of relative abundance from the NMFS spring survey.

The distribution of age 4+ haddock determined by using the catch-per-tow data from the DFO spring survey pooled over 1986 to 1996 and the NMFS spring survey pooled over 1968–71, 1972–84, and 1985–95 are shown in Figure 6. During the 1972–84 and 1985-95 period (1986–96 for the DFO survey) there were aggregations throughout the Canadian side of 5Zj,m, especially in the area of the northeast peak, whereas the U.S. side showed lower abundance. This was especially evident for the 1985–95 period, but there were a number of occurrences of haddock along the southern flank of the bank in this period also. The spring distribution from 1968 to 1971 was markedly different from the recent distribution pattern. The northeast peak aggregations were not seen, and haddock seemed to be distributed uniformly throughout 5Zj,m. The distribution pattern during this period was strongly influenced by the exceptionally abundant 1963 year class.

Instantaneous rates of net migration

Haddock landings by the U.S. and Canadian fisheries have been affected by the spawning closure area

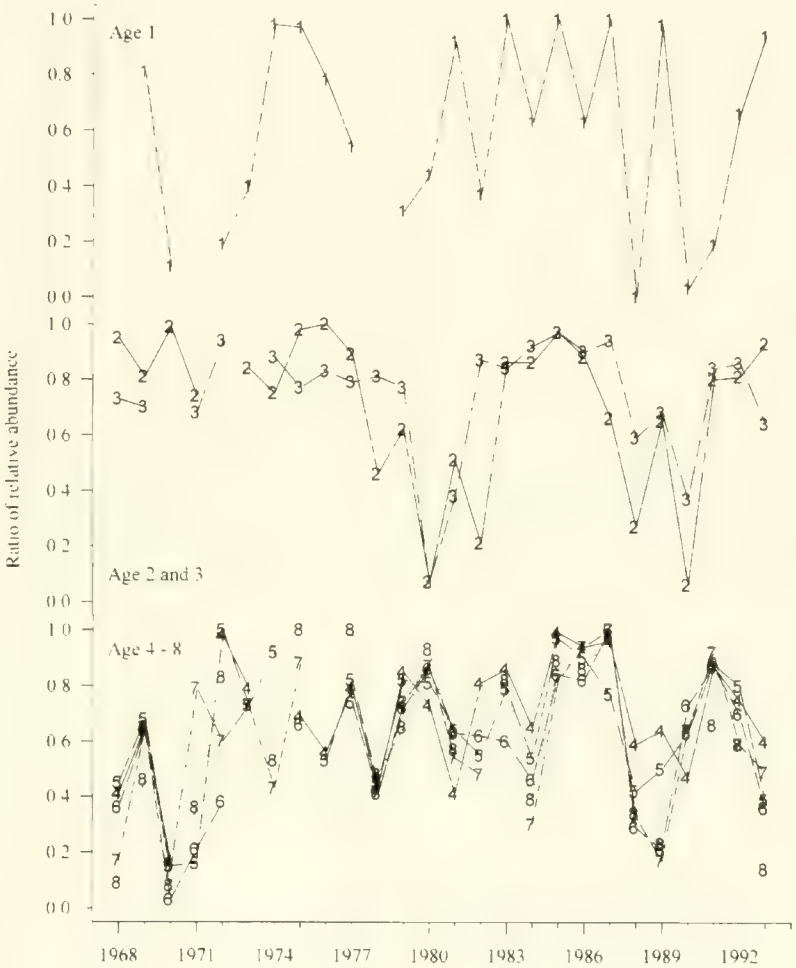

Figure 8

Relative abundance of haddock on the Canadian side of 5Zj,m by age group from the NMFS spring survey. Ratios were determined as abundance on Canadian side to total abundance in 5Zjm.

which was first instituted in 1970 by the International Commission for the Northwest Atlantic Fisheries and which was retained by both countries following extension of jurisdiction in 1977 (Halliday, 1988). The closure, which was put into effect from March to April during 1970–71, was extended to include May in 1972 and at that time an exemption for hook fisheries was introduced. In 1987 the United States extended the period to include February and in 1993, it was further extended to include January through June. The Canadian bottom trawl fishery has traditionally had limited activity during January and February except during 1991–93. Since 1985, when Canada and the United States have conducted haddock fisheries only on their respective sides of the ICJ line, the U.S. monthly catch of haddock in unit areas 5Zj,m (Fig. 9) generally have increased from January to June, but a sharp decline in landings occurred in July and the months following. Canadian landings peaked in June and July, the first two months following the spawning closure period, and decreased gradually to November.

The 6-month net migration rates calculated for three age groups (age 1, ages 2 and 3 combined, and ages 4 to 8 combined) displayed a persistent seasonal pattern indicating net movement towards the U.S. side between October and April followed by a return to the Canadian side between April and October (Fig. 10). Age-1 haddock had the greatest net migration rate to the Canadian side from April to September but also the

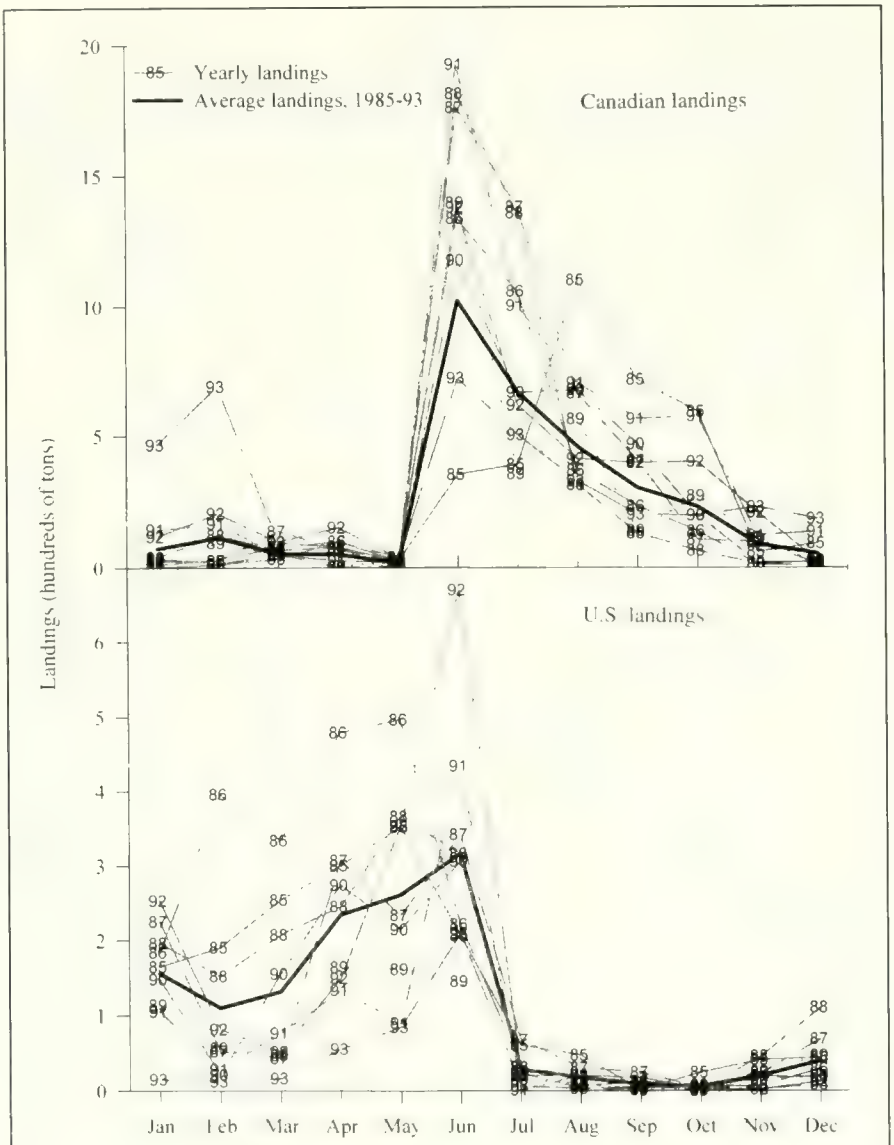

Figure 9

Monthly haddock landings in 5Zj,m from 1985 to 1993.

most variable.The net migration rate towards the U.S. side from October to March was often lowest at age 1, intermediate at ages 2 and 3, and greatest at ages 4 and older. By ages 4+ net migration back and forth seemed to be balanced. This general pattern was supported by the migration rates for the entire period examined, but the trend was less distinct from April 1985 to October 1987 than from April 1988 to October 1993. Examination of the spring ratios of relative abundance showed very high values during 1985–87 for ages 4–8 haddock (Fig. 8), indicating that there was not much movement across the ICJ line during that period.

Figure 11, which shows the movement and removals of a weak and a strong year class, the 1984 and 1985, respectively, for ages 1 and older, illustrates the migratory nature of the 5Zj,m stock across the ICJ line. The migratory pattern is well illustrated; a portion of the stock moved to the U.S. side from October to March and most of the stock moved back to the Canadian side from April to September. In spring the abundance on the Canadian side remained higher than on the U.S. side. The U.S. catch often consisted primarily of fish that had moved across the ICJ line from the Canadian side to the U.S. side and is indicated in the figure by the arrows pointing to the left.

No obvious pattern between net migration rates and population abundance was found. The range of abundance, however, for this period was very limited.

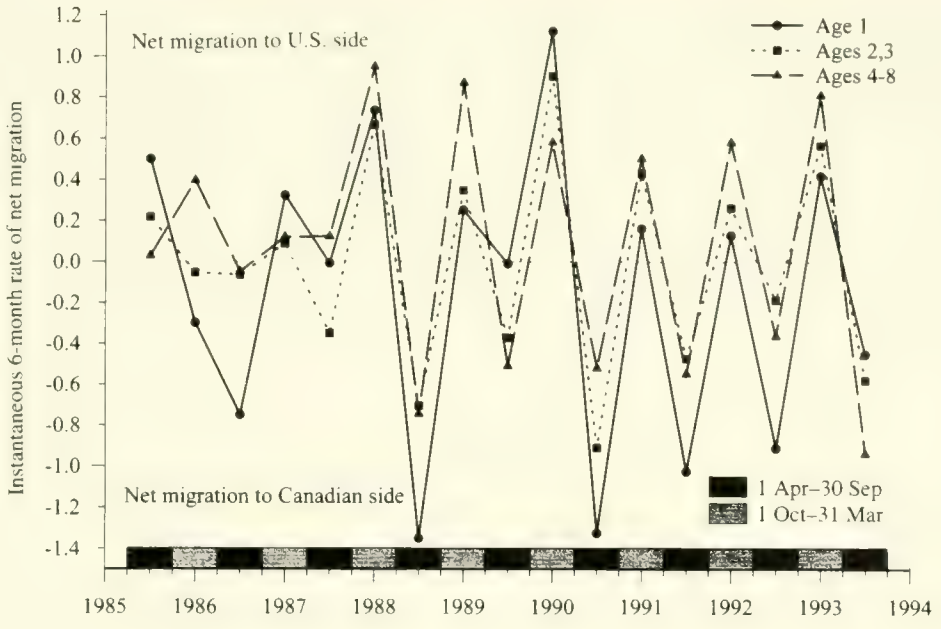

Figure 10

Net migration rates (expressed as annual rates) across the ICJ line for 6-month time periods for 5Zj,m haddock. These rates show that from April to September, net haddock migration was towards the east resulting in almost all haddock in 5Zj,m residing on the Canadian side in the fall. There was then a migration westward and across the ICJ line from October to March, a migration associated with spawning activities.

Discussion

Observations regarding haddock spatial distribution on Georges Bank during an earlier period (Colton, 1955) and for two dominant year classes more recently (Overholtz, 1985) have indicated that adult haddock are more abundant off the bank in deeper waters during the fall but are found on the bank in shallower waters during the spring. Colton (1955) reported that during spring, the greatest concentrations of larger haddock occur in water less than 110 m and presumed this was related to spawning activities. Migration from shallower water in spring to deeper water in the fall appears to occur by the end of July. Colton (1955) reported that few haddock of any age were found between 110 m and 165 m during the July–August surveys undertaken in 1949 and 1950. Older haddock, age 5+, could be found in waters deeper than 165 m in unit areas 5Zg,h and j. Overholtz (1985) also suggested that survey distributions of age-2 haddock indicated a movement by summer to deeper water in relation to the shallower depths generally occupied in spring. Colton (1955) and Overholtz (1985) reported some segregation of ages as fish moved into deeper water, i.e. older fish occupied deeper water than did younger fish, but Colton (1955) observed that in spring there appeared to be less segregation of age groups.

Although we observed two distinct distribution patterns over time within 5Zj,m, our analysis indicates that the depth-related patterns described above were persistent. The 1963–71 distribution pattern will be discussed more fully later in this section. Patterns observed from 1972 to recent times show that adult haddock in 5Zj,m were broadly dispersed over the bank during the spring period, their distribution extending westward of the ICJ line especially along the southern flank of Georges Bank. The NMFS strata with the highest densities in the spring were the Canadian portions of 21 and 16 which have a depth range from 56 to 110 m. The ratios of relative abundance, especially those from the DFO survey, clearly show that the majority of age-2+ haddock occupied waters within the Canadian jurisdiction at that time. Both NMFS and DFO spring surveys exhibit similar distribution patterns with similar areas of concentration. During the fall, haddock distribution shifted to the east onto the deeper bank slopes and few haddock remained on the U.S. side of the ICJ line. The ratios of relative abundance indicate that virtually all age 1+ haddock within 5Zj,m are on the Canadian side of the ICJ line in the fall.

The net migration results suggest that the westward migration of age-2 and older haddock in the winter–spring period is matched by a corresponding eastward migration during the summer–fall period of roughly similar magnitude. The net result is that roughly 20% to 25% of the adult haddock move across the ICJ line during a cycle. There may be a tendency for older haddock to migrate back and forth across the boundary line in greater numbers than for younger haddock because the instantaneous rates of net migration during the winter period for ages 4–8 are often greater than for younger ages, i.e. six out of nine times (Fig. 10). No relationship was found between stock abundance and the 1985–93 spring net migration rates, or the 1968–93 spring ratios of relative abundance, when a greater range in stock abundance occurred. The variability seen in the magnitude of movement to the U.S. side in spring from year to year (Figs. 8 and 10) may reflect variation in the timing of migration, variation in the magnitude of migration, sampling variation, or immigration from another source. Improved understanding of the source of this variability and better estimates of the magnitude and extent of migration may be possible from repeated surveying during the winter–spring period.

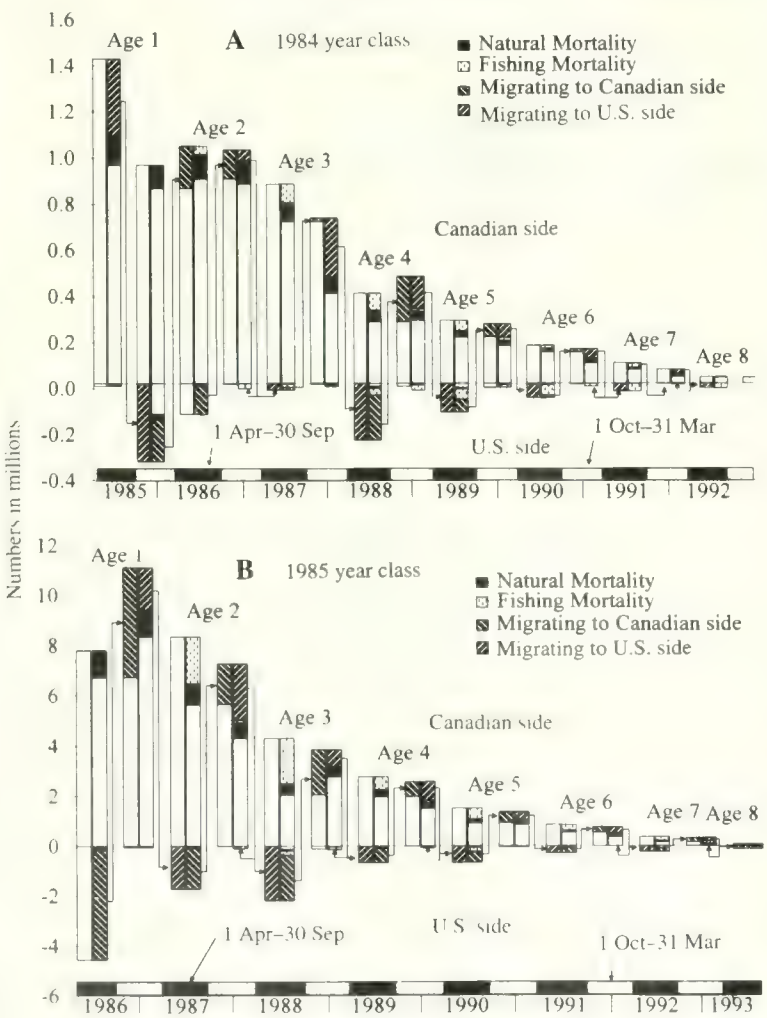

Figure 11

History of the (**A**) 1984 and (**B**) 1985 haddock year classes in unit areas 5Zj,m. The first bar of each pair represents the population size at the beginning of each 6-month period with the numbers gained from migration, if any. The second bar indicates the numbers lost to natural mortality, fishing mortality and migration to the other side of the ICJ line. The number of haddock left over at the end of the time period is represented by the unshaded portion of the second bar. The haddock that migrated across the ICJ line are added to the population or contribute to fishing mortality on the side they are migrating to during the same time period.

Distribution and migration show differences by age. The distribution of age-0 haddock was found to be different from that of older haddock, as has been previously described (Overholtz, 1985; Lough and Boltz, 1989; Polacheck et al., 1992). Haddock eggs and larvae spawned on the northeast peak may be distributed as far south as the Middle Atlantic Bight (Polacheck et. al., 1992). The ratios of relative abundance of age-0 haddock during fall are very variable and abundance often favors the U.S. side. There was a pattern of strong year classes being more abundant on the U.S. side whereas the weak year classes that followed were more abundant on the Canadian side. Additional research is needed to determine whether there is a mechanistic explanation for this observation. Our results suggest that the distribution and movement of age-1, -2 and -3 haddock differ from those of older haddock. In spring there was some correlation of ratios of relative abundance such that age-4 and older haddock had similar patterns and age-2 and age-3 haddock were similar whereas age-1 haddock did not correlate with any other ages. The differences likely reflect different migration patterns of immature and mature haddock. Maturity rates increase from ages 1 to 3 and by age 4 all haddock are mature (O'Brien and Brown, 1996; Trippel et al., 1997).

Haddock biomass (age 2 and older) on all of Georges Bank from 1935 to 1960 averaged 153,000 meteric tons (t). In

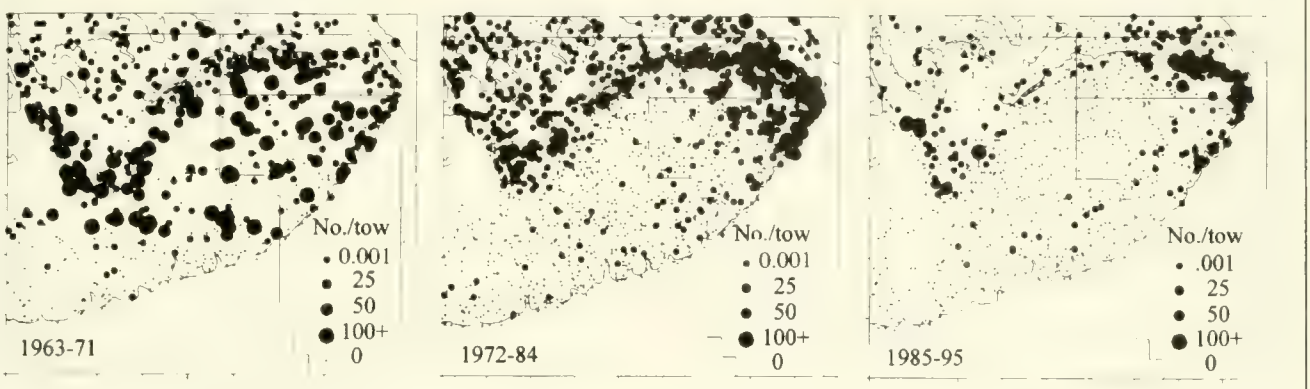

Figure 12

Fall distribution of age 1+ haddock on Georges Bank from NMFS bottom-trawl surveys. Data have been aggregated for the three time periods shown. Note that 1969 data are not included as these data were unavailable.

1965, biomass peaked at 427,000 t due to the recruitment of the "very strong" 1962 and the "outstanding" 1963 year classes that continued to dominate the population during the late 1960s and early 1970s (Clark et al., 1982). There was a large decline, by an order of magnitude, in the biomass of haddock on Georges Bank during the late 1960s and the early 1970s to a low of 14,000 t in 1973 (Clark et al., 1982). The fall distribution pattern during this period of exceptionally high but rapidly decreasing abundance indicates that haddock within 5Zj,m were more widely dispersed over the bank from 1963 to 1971 (Fig. 6) than that which was observed subsequently. Moreover, the ratios of relative abundance did not strongly favor the Canadian side of the ICJ line during 1963–71 (Figs. 4 and 5). This difference in distribution was also evident in the spring distribution pattern for ages 4 to 8 (Fig. 6) and in the spring ratios of relative abundance that were generally less than 0.5 during 1968–71 (Fig. 8). After this period, the ratios, though variable, were usually above 0.5. Polacheck[2] noted that haddock, since the late 1960s, were almost never caught in research survey tows in the southern and central portions of Georges Bank, areas where they had been caught regularly during the mid-1960s.

The post-1971 ratio of relative abundance trends for haddock persist to the present. During the late 1970s and early 1980s, the 1975 and 1978 year classes dominated the population and since then there have been several moderately strong year classes, i.e. the 1983, 1985, 1987, and 1992 (O'Brien and Brown, 1996; Gavaris and Van Eeckhaute, 1997). Despite accompanying fluctuations in haddock abundance, the relative abundance pattern has not reverted to that observed from 1963 to 1971. Polacheck,[2] using percent zero tows and patchiness to explore spatial distribution of Georges Bank haddock, also observed that when abundance increased with the 1975 and 1978 year classes, the patterns in spatial distribution did not resemble those observed from 1963 to the late 1960s. The distribution pattern during that time period was influenced strongly by the exceptionally large 1963 year class and may not be typical of the stock when it was in a more stable state as during the 1935–60 period. Recognizing the two spawning components and the likelihood that haddock may display different spatial affinities depending on their origin, we hypothesize that the 1963–71 distribution patterns may have been the result of an unusually greater contribution of recruitment from the southwestern spawning component. On the other hand, since 1985, the southwestern spawning component has probably been depleted to a greater extent and may not be contributing to Georges Bank production to the degree that it did from the mid-1970s to mid-1980s. The depletion of the southwestern spawning component is well illustrated by the fall distribution in 5Ze of ages 1+ haddock for three time periods, 1963–71, 1972–84, and 1985–95 (Fig. 12). Note that the almost continuous distribution of haddock seen along the northern edge of the bank during the first two time periods is not apparent during the later time period.

Since 1985, the relative abundance across the ICJ line and the net migration rates have likely not been strongly affected by variations in the abundance of the eastern Georges Bank spawning component. However, these attributes may get distorted by dis-

[2] Polacheck, T. 1995. CSIRO, Division of Fisheries, P.O. Box 1538, Hobart, Tasmania 7001, Australia. Personal commun.

tributional overlap of the two spawning components if the abundance of the southwestern component increases. This overlap effect may be responsible for the higher abundance at ages 2 and 3 of the strong 1978 year class on the U.S. side in spring (Fig. 8). Note, however, that at ages 4 and older, abundance shifts to being higher on the Canadian side of 5Zj,m.

From the temporal and spatial patterns of distribution, ratios of relative abundance with respect to the ICJ line, net migration rates, and monthly landings statistics, we can infer then that a seasonal migration, probably associated with spawning behavior, occurs in 5Zj,m. This migratory behavior may be influenced by temperature conditions but, although temperature data is collected during surveys, the time range of this information is too limited to investigate the effect on migration timing. The westward movement of haddock onto the bank into shallower water probably begins around November and reaches its greatest extent to the west during the peak of spawning in March–April, after which the return migration eastwards begins. Most haddock have probably migrated eastward across the ICJ line by July and by October; haddock are found far east of the line preferring the deeper waters of the northeast slopes of the bank.

An understanding and appreciation of the distribution and migration patterns on eastern Georges Bank in relation to the ICJ line are important prerequisites for investigation of sustainable harvest practices for this transboundary resource. The pattern of migration described in our study does not alter sustainable levels for the area as a whole but because of the seasonal nature of exploitation by Canada and the United States, this information can provide guidance on the exploitable biomass available on each side during different seasons so that consistent and equitable harvest rates can be determined. After establishment of the international boundary, Canada and the United States have managed the resources in their respective territories with little attention to what was being done in adjacent waters. Though it has been suggested that sustainable fisheries could be maintained through independent management (Gavaris et al., 1993), it is likely that the greatest potential would be achieved through consistent management. Knowledge of temporal and spatial distribution patterns can form the basis upon which consistent management practices are explored.

Acknowledgments

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Reduction of growth in otoliths of widow and yellowtail rockfish (*Sebastes entomelas* and *S. flavidus*) during the 1983 El Niño

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Abstract.—Growth of otoliths of adult widow rockfish, *Sebastes entomelas*, and yellowtail rockfish, *S. flavidus*, inhabiting the coastal waters off central and northern California was reduced in 1983. This reduction (12.6% and 20.5%, respectively) coincided with a strong El Niño event that dominated oceanographic conditions that year. Otolith growth from 1980 to 1987 was significantly correlated with ocean temperature, upwelling, and sea level anomaly. Specifically, in 1983, the highest ocean temperature, largest positive sea level anomaly, and lowest amount of coastal upwelling corresponded to the smallest mean otolith growth increment.

In 1983, one of the strongest El Niño events of the century occurred in the east-central Pacific Ocean (Cane, 1983; Rasmusson, 1984; Glynn, 1988). This event had strong negative effects on the growth of many marine organisms inhabiting waters along the west coast of North America, including giant kelp (Zimmerman and Robertson, 1985), yellowtail rockfish (Lenarz and Wyllie Echeverria, 1986), coho and chinook salmon (Pearcy and Schoener, 1987), Pacific herring (Spratt, 1987), Pacific kelp (Germann, 1988), Pacific hake (MacLellan and Saunders, 1995), and blue rockfish (VenTresca et al., 1995).

Atypically narrow annuli (annual growth increments) formed during 1983 were observed during routine aging of otoliths from adult yellowtail rockfish, *Sebastes flavidus* (Fig. 1). Because otolith growth is generally proportional to fish growth, a reduction in the width of the 1983 annulus could correspond to poor fish growth caused by the El Niño-induced anomalous oceanographic and biotic conditions present that year. Widths of annually formed increments on the hard parts of animals and plants have been used to correlate growth with a range of environmental conditions. A common example is the relation between the widths of tree rings and annual precipitation. In the marine environment, a reduction in annual shell growth of geoduck clams was observed to correspond with increased pollution (Noakes and Cambell, 1992). Boehlert et al. (1989) used otolith annuli to provide historical time series of growth in *Sebastes* that were compared with environmental factors. In a similar study, MacLellan and Saunders (1995) noted a reduction in the 1983 annulus of Pacific hake otoliths inhabiting northeastern Pacific waters, attributing it to the negative effect of the 1983 El Niño.

In this study, otolith growth from 1980 to 1987 was measured from two commercially important rockfish species: yellowtail rockfish and widow rockfish (*S. entomelas*). These species range from British Columbia to southern California (Gunderson and Sample, 1980). They are semipelagic, associated with bottom structure located on the shelf. The measurements of otolith growth were compared with physical oceanographic variables collected during the same period.

Methods

Otolith growth

Otoliths from female yellowtail rockfish inhabiting Cordell Bank, California (Fig. 2), were collected during research cruises conducted from 1986 to 1992. As noted earlier, during otolith age determination procedures, the 1983 annulus was

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Fish. Bull. 97:680–689 (1999).

observed to be narrower than adjacent annuli. To quantify this observation, measurements of annuli were made on these otoliths, as well as additional otoliths obtained from an ongoing port sampling program. Otoliths were collected from male and female widow and yellowtail rockfish landed at Eureka, California, and female widow rockfish landed at Bodega Bay, California, during 1989 and 1990.

The annulus was defined as otolith growth from the end of one summer to the end of the following summer (approximately October through September). Using reflected light on the distal surface of whole otoliths, I observed that summer growth appears as a white ring and winter growth as a dark ring (Fig. 1). Annuli from 366 otoliths were measured by using one of the two following methods. With the first method, a camera lucida was mounted atop a dissecting microscope, which was used to trace the surface annuli from 115 female yellowtail rockfish otoliths collected at Cordell Bank. A digitizing pad was used to measure the area of each annulus from the tracings. One or two otoliths per hour could be processed with this method. The remaining 251 otoliths were analyzed by using an image enhancement system comprising a personal computer interfaced with a dissecting microscope and a high resolution closed-circuit video camera. A mouse-driven crosshair was used to trace the annuli displayed on the monitor. This method increased production by sixfold. The area of each annulus (mm^2) was square-root–transformed prior to analysis. To compare the two methods, annuli from five otoliths measured by the first method were remeasured by using the second method. The differences in the estimated growth from these five otoliths ranged from 0.2 to 11.4%, with a mean of 2.9%, which represented a minor error compared with observed interannual growth differences.

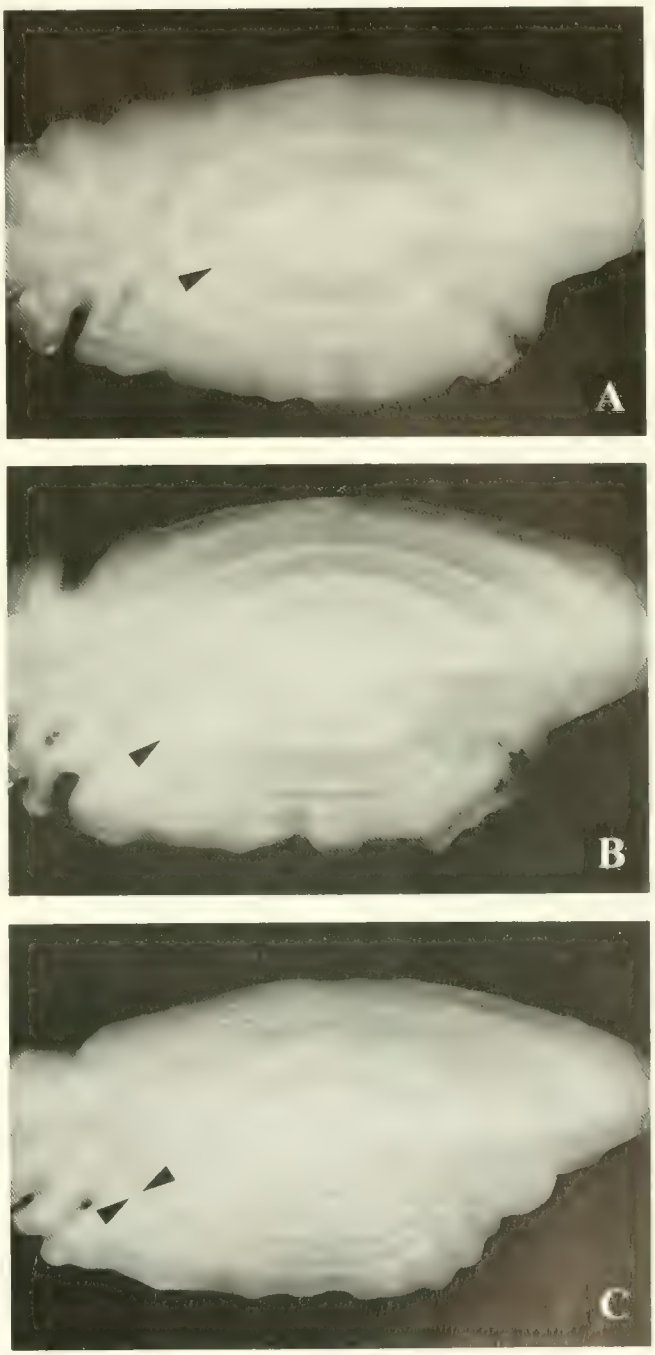

Figure 1

Otoliths from female yellowtail rockfish collected at Cordell Bank, California, showing narrow 1983 annulus (arrow): (**A**) 1982, (**B**) 1981, and (**C**) 1980 year classes.

Potential problems arise when measuring all the annuli in an otolith. When these rockfish species reach sexual maturity and somatic growth slows, the reduced growth rate is reflected in their otoliths. Therefore, it would be impossible to determine if a reduction in otolith growth was caused by poor environmental conditions or from energy being diverted into gonadal development. In addition, annuli formed after the onset of maturity are deposited disproportionately on the proximal surface of the otolith. It is easier to measure annuli deposited during the immature phase on the distal side of the otolith. To minimize these concerns, measurements were restricted to the five annuli formed prior to sexual maturity. Both male and female widow rockfish have an age of 50% maturity of five years, whereas male and female yellowtail rockfish are mature at six and seven years,

Table 1
Sample sizes for each combination of rockfish species, port, sex, and yearclass.

Species	Port	Sex	Yearclass 1979	1980	1981	1982	1983	Total
Yellowtail	Eureka	Female	2	22	10	6	11	51
Yellowtail	Eureka	Male	1	27	19	1	10	58
Yellowtail	Cordell Bank	Female	16	38	47	13	1	115
Widow	Eureka	Female	9	9	22	11	1	52
Widow	Eureka	Male	12	10	21	11	4	58
Widow	Bodega Bay	Female	7	4	15	6	0	32
Total			47	110	134	48	27	366

respectively (Wyllie Echeverria, 1987). An additional concern arises from the protracted parturition season exhibited by these species. Interannual differences in birthdate distributions (Woodbury and Ralston, 1991) result in interannual differences in otolith growth during the first year of life. Therefore, measurements of the first annulus were not included in the analysis because they might have biased the data. Only measurements of otolith growth for the years 1980–87, comprising ages 1–4 and otoliths from fish belonging to the 1979–83 year classes (Table 1) were used.

The results of this study are dependent upon the accuracy of the ages assigned to each otolith. It is not uncommon for ages to vary by one or more years between readers or among readers re-aging the same otolith. The 1983 annulus was observed over a period of several years during which one additional annulus was deposited each subsequent year for year classes prior to 1983. By using the distinctive 1983 annulus (Fig. 1) as a natural tag (MacLellan and Saunders, 1995), I was able to assign an age to each otolith in this study that was accurate.

To test the validity of the 1983 annulus in this study, twelve otoliths that had previously been aged were re-examined without knowledge of their date of capture. On the basis of only the pattern of annuli widths, 11 of the 12 otoliths were assigned to their previously determined year class. The one misinterpretation was for an otolith from a fish born in 1984, which did not have the 1983 annulus. This error would be unlikely in the data used for this study because the otoliths were first aged by the break-and-burn method, in which the year of birth was determined from counting all the annuli. The narrow 1983 annulus could then be used to ensure that the correct age was obtained.

The following additive model (Weisburg, 1993) was used to calculate treatment effects on annual otolith growth for each species over all years.

Figure 2
Sampling locations at Eureka, Bodega Bay, and Cordell Bank.

$$\Delta_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + \varepsilon_{ijkl},$$

where Δ_{ijkl} = index of annual otolith growth of a species;
μ = mean square-root of annual growth;
α_i = year "i" fixed effect;
β_j = age "j" fixed effect;
γ_k = port "k" fixed effect;
δ_l = sex "l" fixed effect; and
ε_{ijkl} = normal error term.

This model assumes no significant interaction among any of the four main effects. This assumption was evaluated in Figures 3 and 4, where annual least-square means are plotted against year for each species-sex-port combination by using both a combined model with no interaction term for the age-by-year

effect, and a model with interactions that estimates a distinct otolith growth effect for each age-by-year combination. These figures show that although there are statistically significant interactions, the signal for the year effect is not strongly effected by excluding the interaction terms from the model. The additional variance explained by the model with interactions was only 3.5% and 4.2%, for yellowtail and widow rockfish, respectively. Because inclusion of an interaction term contributes little to the explanatory power of the model, and analyses that include interaction terms are much more restrictive in terms of data requirements, the simple, combined additive model was used, thereby allowing the computation of a longer time series of annual otolith growth effects (1980–87).

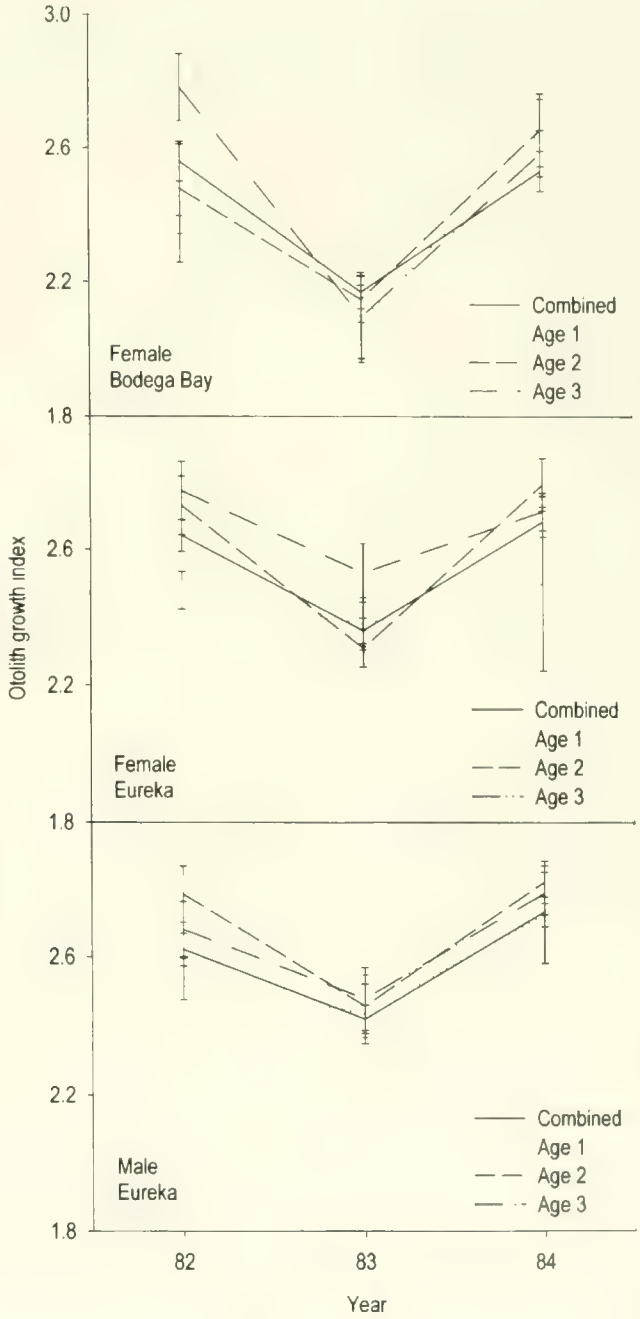

Figure 3

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for widow rockfish. Bars represent ±1 standard error of the mean.

Oceanographic databases

Thirteen oceanographic variables were analyzed to determine their relation with otolith growth patterns. These included eight measures of ocean temperature, three upwelling indices, a sea level statistic, and the northeast Pacific atmospheric pressure index. All ocean temperature data were obtained from the Fleet Numerical Oceanography Center, Master Oceanographic Observations Data Set (Sharp and McClain, 1993). The data included temperature at the sea surface, at 100 m, at 200 m, and the depth of the 10°C isotherm. Measurements were summarized from two coastal areas (i.e. 36–39°N × 121–125°W and 39–42°N × 123–127°W), which together encompass the region where the fish were collected. Annual means for 1980–87 were calculated from the monthly means of October through September, the otolith growth year as defined in this study. Annual upwelling indices (Bakun, 1975) were calculated from daily upwelling statistics. In this instance, the mean of the February to April monthly means was computed, as these three months bracket the spring transition (Strub et al., 1987) when nutrient-rich water is first upwelled to the surface, initiating the biological production cycle (Cushing, 1975). Upwelling data were summarized from three localities (i.e. 36°N, 39°N, and 42°N), which represent the area of fish collections. Sea level data compiled at the San Francisco tidal station were used to compute monthly anomalies, after correcting for differences in atmospheric pressure (University of Hawaii[1]). Annual mean sea level anomalies were then calculated from the monthly means of October through September. Lastly, the northeast Pacific atmospheric pressure index is an indicator of atmospheric forcing upon ocean waters (Beamish and Bouillon, 1993). This index is the mean monthly difference in surface atmospheric pressure between 40°N, 120°W (Reno,

[1] Sea Level Center, Univ. Hawaii, Honolulu, Hawaii. 1994. Unpubl. data.

Nevada) and 50°N, 170°W (Aleutian Islands) (NOAA[2]). A plot of the data revealed an increase in the intensity of the pressure differences during the winter months. Therefore, annual means were calculated from the monthly means for November to March.

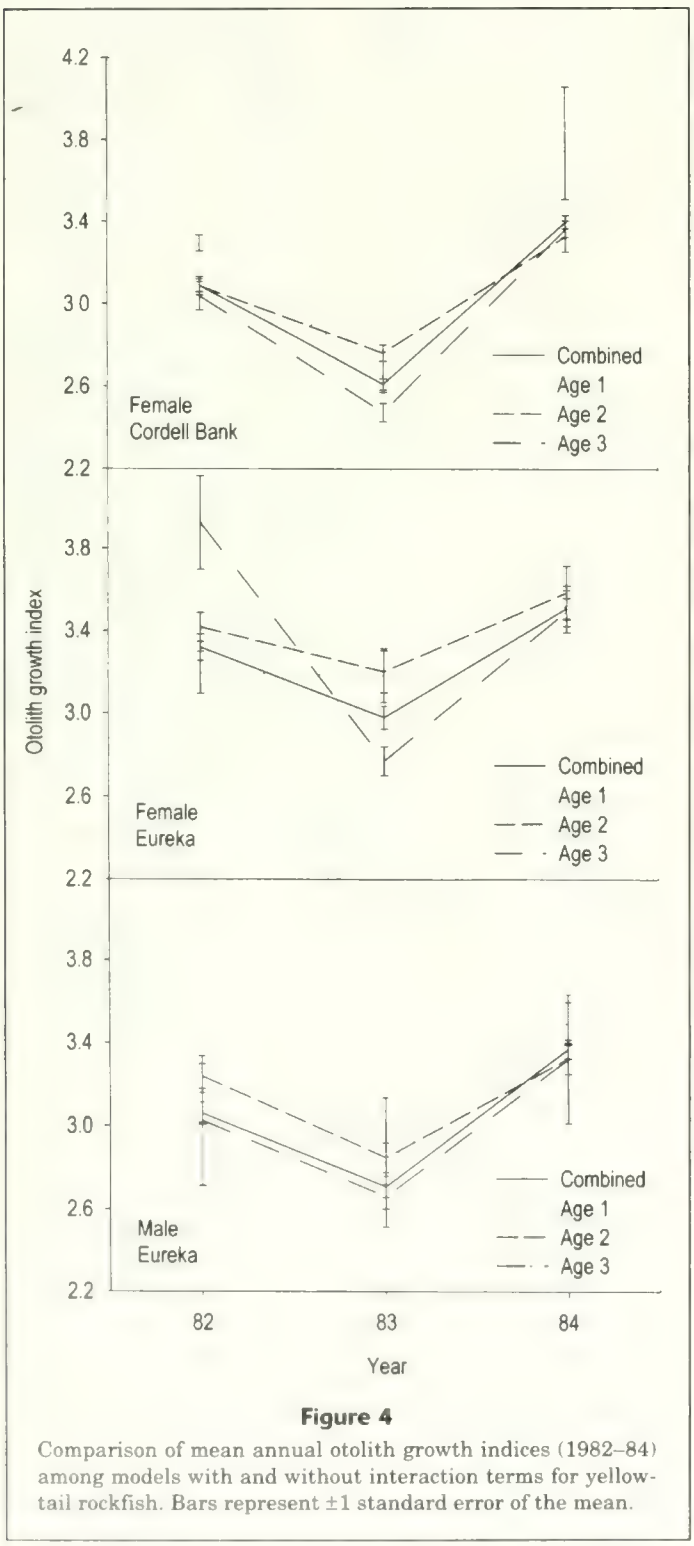

Figure 4

Comparison of mean annual otolith growth indices (1982–84) among models with and without interaction terms for yellowtail rockfish. Bars represent ±1 standard error of the mean.

Owing to strong interdependence among these 13 oceanographic variables, a principal component analysis (SAS Institute Inc., 1988) was conducted to reduce the dimensionality of the information and to insure statistical independence of the data. The ordination was conducted on the correlation matrix, so that each variable was weighted equally. The otolith data were then compared with the principal components of the oceanographic data to quantify the impact of the 1983 El Niño event on the growth of yellowtail and widow rockfish otoliths.

Results

Patterns of annual otolith growth were similar in widow and yellowtail rockfish from 1980 to 1987 (Fig. 5). A 12.6% and 20.5% reduction in otolith growth occurred during 1983 for widow and yellowtail rockfish, respectively. This year of reduced otolith growth was followed by enhanced growth, especially for yellowtail rockfish. The growth estimates calculated for 1980 and 1987 were based on samples from one year, i.e. the 1979 and 1983 year classes respectively, and these estimates should be viewed with caution.

Although most of the variance in otolith growth is explained by the year effect, the other effects in the model are worth noting (Table 2). There was a significant difference in otolith growth between sexes for yellowtail rockfish (i.e. otoliths from females grew faster than those from males); however, this was not the case for widow rockfish. Growth of the otolith at age differs between species (Fig. 6), which may be the result of somatic growth rate differences between the species. In a simple simulation, similar curves were produced by varying the von Bertalanffy growth coefficient (k). Yellowtail rockfish exhibit faster growth than do widow rockfish, thus yielding relatively lower indices of otolith growth with increasing age. There was a significant difference in otolith growth between the two ports for both species (i.e. otoliths from fish collected in Eureka grew faster than those from Bodega). Further analysis revealed that these differences began in 1983. Figure 7 shows results of four separate ANOVAs run on each of the four species-port combinations. In these analyses, sex and port were excluded as effects in the model. Otolith growth was similar at the two ports prior to 1983. Al-

[2] Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, Washington. 1994. Unpubl. data.

Table 2

Analysis of variance results for the growth model used in this study.

Source	df	Sum of squares	Mean square	*F*-Value	*P*>*F*
Widow rockfish (r^2=0.318)					
Model	12	19.9617	1.6635	21.57	0.0001
Year	7	13.6558	1.9508	25.29	0.0001
Age	3	2.3318	0.7773	10.08	0.0001
Port	1	0.9860	0.9860	12.78	0.0004
Sex	1	0.1064	0.1064	1.38	0.2408
Error	555	42.8046	0.0771		
Corrected total	567	62.7663			
Yellowtail rockfish (r^2=0.542)					
Model	12	96.8742	8.0728	87.09	0.0001
Year	7	77.8370	11.1196	119.96	0.0001
Age	3	3.3136	1.1045	11.92	0.0001
Port	1	3.5704	3.5704	38.52	0.0001
Sex	1	3.8560	3.8560	41.60	0.0001
Error	883	81.8491	0.0927		
Corrected total	895	178.7233			

though both species exhibited significant reduction in otolith growth in 1983, the effect was more pronounced at Bodega, consistent with a decreasing effect of El Niño with increasing latitude, as was observed in Pacific hake (MacLellan and Saunders, 1995). Although otolith growth recovered quickly for both species at Eureka and for yellowtail rockfish at Bodega, otolith growth for widow rockfish collected from Bodega was relatively slow to recover.

Results of the principal component analysis on the oceanographic data (Table 3) show that only the first two components are very informative (eigenvalue ≥1; first three principal components shown). Note that the first component explained 70% of the combined variation among all 13 oceanographic variables, whereas the second component accounted for an additional 18%. As the loadings on the first principal component indicate, temperature and sea level anomaly are closely linked. Upwelling loads higher with increasing latitude, which may relate to increased upwelling from south to north along that section of coast. Upwelling also demonstrates an inverse relation with temperature and sea level anomaly. Finally, the atmospheric pressure statistic does not contribute substantially to the first principal component, although it is much more influential in the second component.

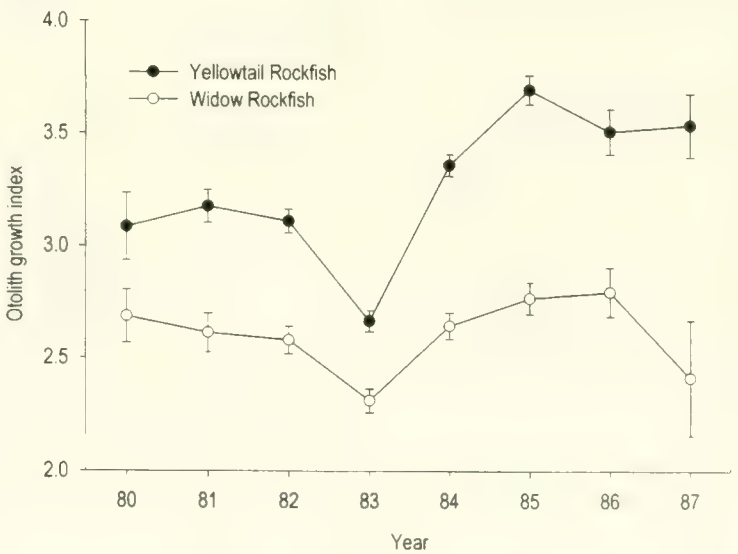

Figure 5

Mean annual otolith growth indices (1980–87) for each species. Bars represent ±2 standard errors of the mean.

A multiple regression of otolith growth on the first two principal components showed that the second component was neither significant nor informative, and it was therefore dropped from the analysis. An ordinary regression of otolith growth on the first principal component resulted in a significant relationship for both widow and yellowtail rockfish (P=0.033

and 0.030, respectively). Plots of mean annual otolith growth index against the first principal component score (Fig. 8) reveal the extreme conditions that prevailed in 1983. In 1983, the lowest measurements of otolith growth corresponded to the highest sea temperature, highest positive sea level anomaly, and lowest upwelling index. As previously noted, this particular El Niño was one of the strongest on record for the east-central Pacific Ocean. Its signature was noted off the California coast by high sea temperature at 100 m, being the warmest observed since records were first kept starting in 1944 (Sharp and McClain, 1993). A converse relationship between enhanced otolith growth and lower sea temperature, lower sea level anomaly, and higher upwelling index is not as evident, although above normal growth did occur in 1985, which was the "coldest" year.

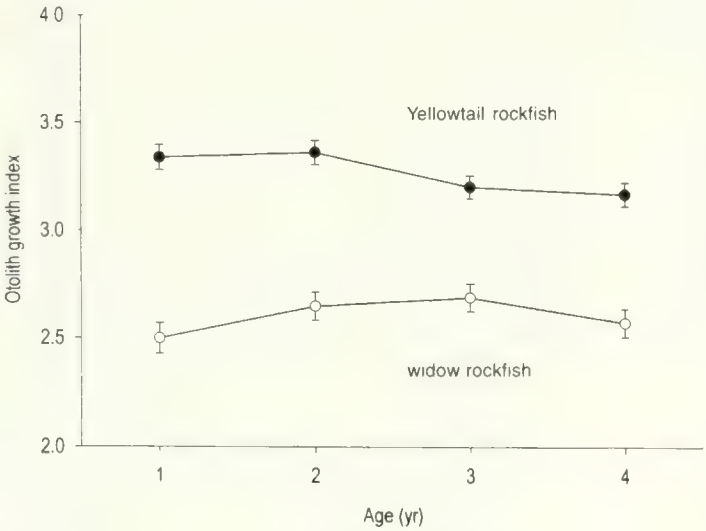

Figure 6

Mean otolith growth indices at age for widow and yellowtail rockfish. Bars represent ±2 standard errors of the mean.

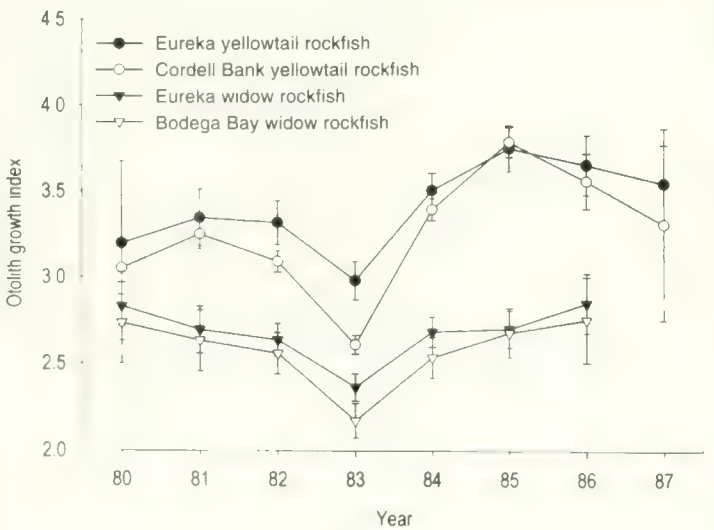

Figure 7

Mean annual otolith growth indices (1980–87) for widow and yellowtail rockfish from two geographic areas. Bars represent ±2 standard errors of the mean.

Discussion

In this paper, the reduction in growth of widow and yellowtail rockfish otoliths during 1983 was quantified by measuring annuli surface areas. Otolith growth is postulated to represent a conservative measure of somatic growth. Casselman (1990) determined that otoliths from several species of freshwater fish grew relatively faster than their body during periods of slow body growth. Francis et al. (1993) argue that otolith growth in *Pagrus auratus* can occur even if somatic growth has stopped. Therefore, the reduction observed from this study may indicate an even larger reduction in somatic growth, perhaps affecting reproductive capacity as well. This was observed by VenTresca et al. (1995) who noted a reduction in both the somatic and gonadal indices of blue rockfish (*S. mystinus*) inhabiting California coastal waters in 1983.

It appears that the oceanographic perturbations caused by El Niño had a negative effect on the growth of these fish. Temperature has been implicated as a major contributor to influencing both otolith and somatic growth. Lombarte and Lleonart (1993) stated that environmental conditions, mainly temperature, regulate the quantity of material deposited during the formation of the otoliths. Dorn (1992) found that growth of Pacific whiting (*Merluccius productus*), which inhabit similar waters, is most affected by temperature during younger ages.

Although physical oceanographic conditions and otolith growth were found to be significantly correlated, the causal relationship may well be based on preferred food availability. Central California represents the southernmost range of both widow and yellowtail rockfish. Pearson and Hightower (1991) reported slower

growth of widow rockfish in this area as compared with growth from more northerly distributed populations. This may be related to diet because more northerly distributed populations consume more fish and euphausiids, whereas populations in the south feed more on gelatinous zooplankters. Lorz et al. (1983) reported the diet of yellowtail rockfish in Queen Charlotte Sound comprised both fish and euphausiids, whereas off Washington it comprised mainly euphausiids. Pereyra et al. (1969) found that fish dominated the diet of both yellowtail and widow rockfish collected near Astoria Canyon, off northern Oregon. Brodeur and Pearcy (1984) noted that yellowtail rockfish preyed on a diverse assemblage, dominated by euphausiid, fish and squid, depending on the season. Adams (1987) reported that widow rockfish collected off northern California fed primarily on gelatinous zooplankters. At Cordell Bank, during late fall, winter, and in years of reduced productivity (e.g. 1983), yellowtail rockfish have been found to feed primarily on gelatinous zooplankton, which has a lower nutritional value than their preferred diet of euphausiids (MacFarlane[3]). Owing to the lack of upwelling and reduced productivity during 1983, these fish were probably forced to feed on less nutritional prey. Although lacking stomach analysis data for 1983, Lenarz and Wyllie Echeverria (1986) found a significant reduction in visceral fat of yellowtail rockfish collected at Bodega Bay during 1983 as compared with 1980, a "normal" year.

An assumption of this study is that the widow and yellowtail rockfish sampled during this study did not migrate to less productive waters during 1983 and then return. Most species within the *Sebastes* genus spend their adult life within a relatively small area (Stanley et al., 1994). Both widow and yellowtail rockfish lead an epibenthic schooling existence, inhabiting the area above benthic structures. Several tagging studies have been conducted on yellowtail rockfish to study the movement of these fish. Carlson and Haight (1972) noted homing behavior in yellowtail rockfish that were captured and transplanted to different areas in Alaska. Pearcy (1992) tagged 25 yellowtail rockfish on Heceta Bank off central Oregon and noted little displacement during a one-month period. However, Stanley et al. (1994) noted displacement of several tagged yellowtail rockfish from Alaskan and Canadian waters after they had been at large for several years. Although no tagging studies have been conducted on widow rockfish, it is worth noting

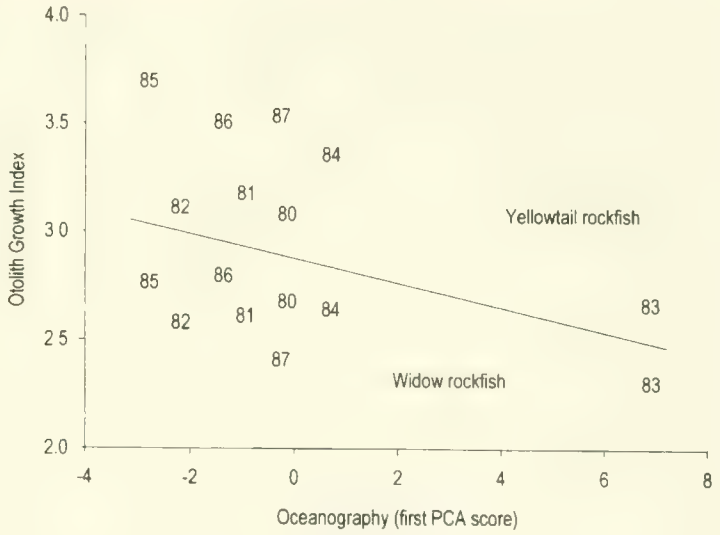

Figure 8

Mean annual otolith growth indices compared to the first principal component annual scores of oceanographic variables.

Table 3

Principal component analysis results for the thirteen oceanographic variables (1980–87).

	Principal component		
	1	2	3
Eigenvalue	9.10	2.36	0.96
Percent variance	70.0	18.1	7.4
Cumulative variance	70.0	88.1	95.5
Eigenvectors			
Sea surface temp at 39–42°N	0.259	0.269	–0.417
Sea surface temp at 36–39°N	0.287	0.255	–0.265
100 m temp at 39–42°N	0.313	0.119	0.276
100 m temp at 36–39°N	0.304	0.053	0.382
200 m temp at 39–42°N	0.302	–0.135	–0.321
200 m temp at 36–39°N	0.301	–0.165	–0.299
Depth of 10°C isotherm at 39–42°N	0.301	0.259	0.129
Depth of 10°C isotherm at 36–39°N	0.301	0.141	0.349
Sea level anomaly	0.296	–0.214	0.296
Upwelling index at 42°N	–0.321	–0.135	–0.024
Upwelling index at 39°N	–0.271	0.357	0.035
Upwelling index at 36°N	–0.148	0.524	0.238
Atmospheric pressure index	0.109	0.498	-0.239

[3] MacFarlane, R. B. 1994. Tiburon Laboratory, NMFS, 3150 Paradise Dr., Tiburon, CA. Personal commun.

that otoliths collected from fish sampled from southern California to British Columbia show distinct growth patterns, indicating little large-scale movement.

One of the best applications of the anomalous 1983 annulus is its use as a chronological marker to improve the accuracy of assigned ages, thus increasing the veracity of age-structured models used in stock assessments (MacLellan and Saunders, 1995). Although the narrow 1983 annuli was most pronounced on young fish at the time of the event, the ring was easily discerned from older fish when their otoliths were broken, burnt, and viewed with reflected light. Therefore, it could be used for decades to aid in the accurate determination of ages of fish born prior to 1983 (Boehlert et al., 1989).

Although the poor environmental conditions present during 1983 appeared to have detrimental effects on the growth of widow and yellowtail rockfish, the effects were short-lived as noted in the increased otolith growth the following years, especially for yellowtail rockfish. As these fish are long-lived (for decades), they have the capacity to absorb occasional years of lower productivity without permanent detrimental effects on the population.

Acknowledgments

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General age- and time-dependent growth models for animals

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Abstract.– Most growth models are age-dependent only. Although their modifications can be used to consider, implicitly, the seasonal growth of animals and the effects of tagging, a general framework is unavailable for explicitly incorporating time and time-dependent factors (i.e. ambient temperature and food availability) in age-dependent growth models. In this paper, I derived general age- and time-dependent growth models for animals and gave a comprehensive list of special cases for age- and time-dependent growth models of von Bertalanffy, logistic, and Gompertz types. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. length increments at age and time increments data from tagging studies), the effects of tagging, and the effects of many population characteristics. I also examined their data requirements, their independence of the start of time and adjustment of estimates of parameters essential for ensuing applications, and concluded that age- and time-dependent growth models are useful for subsequent applications, if and only if they are independent of the start of time or time-homogeneous and if estimates of their parameters are properly adjusted. A scheme for such an adjustment is proposed and demonstrated. Finally, I used nine special cases of these general models to analyze tagging data on a centropomid perch (*Lates calcarifer* (Bloch)). Such analyses suggested that tagging is antagonistic to fish growth and leads to a shrinkage of size and that *L. calcarifer* exhibits a strong seasonality in growth, namely its length grows fastest at the start of autumn, grows less until a full stop in the middle of winter, shrinks until the middle of spring, and resumes a positive growth for another cycle.

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Fish. Bull. 97:690–701 (1999).

Most growth models relate an animal's size to its age alone, are independent of time, and are meant to be useful at all times. Some factors (e.g. ambient temperature and food availability) that are known to affect the growth of animals vary with time, however. Consequently, time has been incorporated in age-dependent growth models implicitly, to consider seasonal (Pitcher and Macdonald, 1973; Appeldoorn, 1987; Smith and McFarlane, 1990; Pauly et al., 1992; Pauly and Gaschütz[1]) and biphasic (Soriano et al., 1992) growth of animals, and the effects of tagging (Xiao, 1994). Xiao's (1996, equations 3.0–4.2, p. 1676–1677) deterministic extensions of the classical von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models also serve these purposes. Similarly, Wang (1998) derived a set of age- and time-dependent growth models for a special case of the von Bertalanffy (1938) growth equation and even constructed distribution-free and consistent estimating functions for estimating their parameters. Although these implicit age- and time-dependent growth models can describe a set of data better than age-dependent growth models, a general framework is unavailable for an explicit incorporation of time and time-dependent factors.

However, an explicit entry of age, time, and time-dependent factors into growth models is essential for studying the effects of many characteristics of a population (e.g. its age composition, size composition, density, and size- or age-specific mortalities) on the growth of its individuals (Moulton et al., 1992; Walker et al., 1998). Indeed, much insight can be gained by examining density-dependent growth alone. This is because density-dependent growth can be effected by 1) compensatory decreases in natural mortality, which may result from a decrease in predation, cannibalism, competition or diseases; 2) compensatory increases in fecundity when food is more readily available or fetal mortality decreases; and 3) compensatory increases in growth rate when more food induces earlier maturity and greater fecundity for each age class (Holden, 1973). For these studies to be feasible, equations for the sizes of individual animals at age a at time t in a population must be coupled with those of their numbers at age a (or size) at time t.

Just as an increase in dimension can reveal new horizons, an explicit incorporation of time and time-dependent factors in age-dependent growth models can be of great use and promise. It also poses interesting philosophical and practical problems. Indeed, in general, time-dependency makes age- and time-

[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES Council Meeting 1979/G:24, 26 p.

dependent growth models depend on the start of time and thereby renders them useless, unless the start of time is known. Of course, the start of time (if it did start at all) is unknown (although some may settle for the Big Bang) and remains a subject of philosophical debate. It is obvious, then, that, for practical purposes, workable age- and time-dependent growth models must be independent of the start of time. But, under what conditions are they so? How should estimates of their parameters be adjusted to make these models useful for subsequent applications at all times? To answer these questions, both age and time must enter a growth equation, explicitly.

In this paper, I derive general age- and time-dependent growth models for animals and give a comprehensive list of special cases for age- and time-dependent von Bertalanffy (1938), logistic (Verhulst, 1838), and Gompertz (1825) growth models. Such models explicitly incorporate age, time, and their dependent factors and are useful for modeling growth at age and time (e.g. from length-at-age data), incremental growth at age and time increments (e.g. from length increments at age and time increments from tagging studies), the effects of tagging, and the effects of population characteristics. I also examine their data requirements, their independence of the start of time, and adjustment of estimates of their parameters for ensuing applications. Finally, I use nine special cases of these general models to analyze data on length increments at age and time increments from a tagging study of a centropomid perch (*Lates calcarifer* (Bloch)) in the Northern Territory, Australia.

General age- and time-dependent growth models

Just as a formal derivation of age-dependent growth models necessitates use of ordinary differential equations, a formal derivation of age- and time-dependent growth models entails use of partial differential equations. This is because both age and time must be taken into explicit account. Readers unfamiliar with first order partial differential equations may wish to skip immediately to Equations 6–6.3, 10–10.3, and 14–14.3, with little loss of comprehension.

Now, let $0 \le y(a,t) < \infty$, $-\infty < a_0 \le a < \infty$, $0 \le t_0 \le t < \infty$, denote the size of an individual of a species of animal of age a at time t, with an arbitrary reference age a_0 and an arbitrary reference time t_0. Suppose that the change in its size at age a at time t in a small time interval of length Δt is proportional to a function of $y(a,t)$ and Δt, such that

$$y(a + \Delta a, t + \Delta t) - y(a,t) = K(a,t) f(y(a,t)) \Delta t,$$

where $K(a,t)$ is its instantaneous rate of growth in size at age a and time t, and can capture the effects of age, time, and their dependent factors. Dividing both sides of this equation by Δt, Taylor series expansion of $y(a+\Delta a, t+\Delta t)$ in the neighbourhood of (a,t) as

$$y(a + \Delta a, t + \Delta t) = y(a,t) + \frac{\partial y(a,t)}{\partial a} \Delta a + \frac{\partial y(a,t)}{\partial t} \Delta t + O(\Delta t),$$

passing to the limit $\Delta t \to 0$, assuming that

$$\lim_{\Delta t \to 0} O(\Delta t) \to 0,$$

and assuming further that

$$\frac{da}{dt} = 1,$$

yield a first order partial differential equation

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t) f(y(a,t)). \tag{1}$$

To solve this equation, I use the following approach. Suppose that the solution of $y(a,t)$ is known. Let $a = t + c$, or $c = a - t$, then

$$w_c(t) = y(t+c,t) \qquad t \ge t_c = \max(t_0, a_0 - c)$$

for a fixed value of $c \in R$. Because $y(a,t)$ satisfies Equation 1, we obtain

$$\frac{dw_c(t)}{dt} = K(t+c,t)f(w_c(t)). \qquad t \geq t_c \tag{2}$$

Equations 1 and 2 are too general to be solved analytically. Now, I examined three of their special cases for $f(y(a,t))$. For each of these special cases, Table 1 describes where to find equations corresponding to various quantities of interest, and Table 2 describes where to find equations corresponding to various special cases of the solution for $y(a,t)$.

Age- and time-dependent growth models of von Bertalanffy (1938) type I

If $f(y(a,t))=y_{max}(a,t)-y(a,t)$, Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a} + \frac{\partial y(a,t)}{\partial t} = K(a,t)\left[y_{\max}(a,t) - y(a,t)\right] \tag{3}$$

$$\frac{dw_c(t)}{dt} = K(t+c,t)\left[y_{\max}(t+c,t) - w_c(t)\right]. \qquad t \geq t_c \tag{4}$$

Of its many interpretations, $y_{max}(a,t)$ can represent the asymptotic size of an average individual as age approaches infinity.

Solution of Equation 4 as an initial value problem with $w_c(t)\,|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c)e^{\int_{t_c}^{t} K(s+c,s)\,ds} + \int_{t_c}^{t} K(s+c,s)\,y_{\max}(s+c,s)\,e^{\int_{s}^{t} K(\zeta+c,\zeta)\,d\zeta}\,ds. \qquad t \geq t_c \tag{5}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0)\,e^{\int_{t-a+a_0}^{t} K(s+a-t,s)\,ds} + \int_{t-a+a_0}^{t} K(s+a-t,s)\,y_{\max}(s+a-t,s)\,e^{\int_{s}^{t} K(\zeta+a-t,\zeta)\,d\zeta}\,ds & a-a_0 < t \\ y(t_0+a-t,t_0)\,e^{\int_{t_0}^{t} K(s+a-t,s)\,ds} + \int_{t_0}^{t} K(s+a-t,s)\,y_{\max}(s+a-t,s)\,e^{\int_{s}^{t} K(\zeta+a-t,\zeta)\,d\zeta}\,ds. & a-a_0 \geq t \end{cases} \tag{6}$$

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 6, then

Table 1

Equations corresponding to various quantities of interest for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Quantity	VB type I	VB type II	Gompertz
Partial derivative of $y(a,t)$	Equation 3	Equation 7	Equation 11
Derivative of $w_c(t)$	Equation 4	Equation 8	Equation 12
Solution for $w_c(t)$	Equation 5	Equation 9	Equation 13
Solution for $y(a,t)$	Equation 6	Equation 10	Equation 14

Table 2

Equations corresponding to various special cases of the solution for $y(a,t)$ for von Bertalanffy (type I) (VB type I), von Bertalanffy (type II) (VB type II), and Gompertz growth equations.

Assumption about $y_{max}(a,t)$	Assumption about $K(a,t)$	VB type I	VB type	II Gompertz
none	none	6	10	14
$y_{max}(a,t)$=constant	none	6.0	10.0	14.0
$y_{max}(a,t)$=constant	$K(a,t)$=constant	6.1	10.1	14.1
$y_{max}(a,t)$=constant	$K(a,t)=K_0+A\cos\frac{2\pi}{T}(t-t_\phi)$	6.2	10.2	14.2
$y_{max}(a,t)$=constant	$K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(a-a_0)/a}$ if $a-a_0<t$; $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/a}$ if $a-a_0\geq t$	6.3	10.3	14.3

$$y(a,t)=\begin{cases} y_{\max}-\left[y_{\max}-y(a_0,t-a+a_0)\right]e^{\int_{t-a}^{t}K(s+a-t,s)ds} & a-a_0<t \\ y_{\max}-\left[y_{\max}-y(t_0+a-t,t_0)\right]e^{\int_{t_0}^{t}K(s+a-t,s)ds} & a-a_0\geq t \end{cases} \tag{6.0}$$

If $K(s+a-t,s)$=K_0=constant in equation 6.0, then

$$y(a,t)=\begin{cases} y_{\max}-\left[y_{\max}-y(a_0,t-a+a_0)\right]e^{K_0(a-a_0)} & a-a_0<t \\ y_{\max}-\left[y_{\max}-y(t_0+a-t,t_0)\right]e^{K_0(t-t_0)} & a-a_0\geq t \end{cases} \tag{6.1}$$

which is the age- and time-dependent von Bertalanffy (1938) growth model, or (if $a-a_0$ or $t-t_0$ is interpreted as time at liberty) Fabens (1965) growth model, with parameters K_0 and y_{max}.

Since many factors (e.g. ambient water temperature and food availability) vary seasonally, the instantaneous rate of growth of many animals $K(a,t)$ fluctuates seasonally. If data are available on $K(a,t)$ as a function of these factors, their relationships can be hypothesized. In reality, however, few such data are available. Nonetheless, one can still hypothesize about a temporal trend in $K(a,t)$ and attribute it to the combined effects of all responsible factors. For example, as a first approximation, $K(a,t)$ is seasonal because of seasonal changes in ambient water temperature and food availability and can be approximated by a sine or cosine curve. Thus, if

$$K(s+a-t,s)=K_0+A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 6.0, an application of the trigonometric function-difference relation

$$\sin(\alpha)-\sin(\beta)=2\cos\left(\frac{1}{2}(\alpha+\beta)\right)\sin\left(\frac{1}{2}(\alpha-\beta)\right)$$

gives

$$y(a,t)=\begin{cases} y_{\max}-\left[y_{\max}-y(a_0,t-a+a_0)\right]e^{K_0(a-a_0)+\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(a+a_0)\right)} & a-a_0<t \\ y_{\max}-\left[y_{\max}-y(t_0+a-t,t_0)\right]e^{-K_0(t-t_0)+\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_0)\cos\frac{2\pi}{T}\left(t-t_\phi-\frac{1}{2}(t+t_0)\right)} & a-a_0\geq t \end{cases} \tag{6.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

Many species of animals are tagged for a variety of purposes. Tagging can affect the growth of some animals positively, neutrally, or negatively. Indeed, some animals may slow down their growth, cease their growth, or even shrink in size after tagging. A proper functional form of $K(a,t)$ is needed to infer these consequences of tagging. If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/a}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/a}$ if $a-a_0\geq t$ in Equation 6.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases} y_{\max}-\left[y_{\max}-y(a_0,t-a+a_0)\right]e^{K_{\max}(a-a_0)+\alpha(K_{\max}-K_{\min})\left(e^{-\alpha(a-a_0)}-1\right)} & a-a_0<t \\ y_{\max}-\left[y_{\max}-y(t_0+a-t,t_0)\right]e^{K_{\max}(t-t_0)+\alpha(K_{\max}-K_{\min})\left(e^{-\alpha(t-t_0)}-1\right)}, & a-a_0\geq t \end{cases} \tag{6.3}$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified. Clearly, the functional form of $K(a,t)$ serves its purpose well. This is because $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals; and $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging.

Age- and time-dependent growth models of von Bertalanffy (1938) type II

If

$$f(y(a,t))=\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^p\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a}+\frac{\partial y(a,t)}{\partial t}=K(a,t)\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^p\right] \tag{7}$$

$$\frac{dw_c(t)}{dt}=K(t+c,t)\frac{w_c(t)}{p}\left[1-\left(\frac{w_c(t)}{y_{\max}(t+c,t)}\right)^p\right], \qquad t\geq t_c \tag{8}$$

Solution of Equation 8 (a Bernoulli's equation) as an initial value problem with $w_c(t)|_{t=t_c}=w_c(t_c)$ yields

$$w_c(t)=\left[\frac{1}{w_c(t_c)^p}e^{\int_{t_c}^{t}K(s+c,s)ds}+\int_{t_c}^{t}\frac{K(s+c,s)}{y_{\max}(s+c,s)^p}e^{\int_{s}^{t}K(\xi+c,\xi)d\xi}ds\right]^{1/p}, \qquad t\geq t_c \tag{9}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0\geq t$, then $c\geq 0$, $-c\leq 0$, then $t_c=t_0$. In other words,

$$y(a,t)=\begin{cases}\left[\frac{1}{y(a_0,t-a+a_0)^p}e^{\int_{t-a+a_0}^{t}K(s+a-t,s)ds}+\int_{t-a+a_0}^{t}\frac{K(s+a-t,s)}{y_{\max}(s+a-t,s)^p}e^{\int_{s}^{t}K(\xi+a-t,\xi)d\xi}ds\right]^{1/p} & a-a_0<t \\ \left[\frac{1}{y(t_0+a-t,t_0)^p}e^{\int_{t_0}^{t}K(s+a-t,s)ds}+\int_{t_0}^{t}\frac{K(s+a-t,s)}{y_{\max}(s+a-t,s)^p}e^{\int_{s}^{t}K(\xi+a-t,\xi)d\xi}ds\right]^{1/p}. & a-a_0\geq t\end{cases} \tag{10}$$

If $p=1$, Equations 7–10 and their special cases are reduced to age- and time-dependent growth models of logistic (Verhulst, 1838) type.

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 10, then

$$y(a,t)=\begin{cases}\left[\frac{1}{y_{\max}^p}-\left(\frac{1}{y_{\max}^p}-\frac{1}{y(a_0,t-a+a_0)^p}\right)e^{\int_{t-a+a_0}^{t}K(s+a-t,s)ds}\right]^{1/p} & a-a_0<t \\ \left[\frac{1}{y_{\max}^p}-\left(\frac{1}{y_{\max}^p}-\frac{1}{y(t_0+a-t,t_0)^p}\right)e^{\int_{t_0}^{t}K(s+a-t,s)ds}\right]^{1/p}. & a-a_0\geq t\end{cases} \tag{10.0}$$

If $K(s+a-t,s)=K_0$=constant in Equation 10.0, then

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{K_0(a-a_0)}\right]^{1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{K_0(t-t_0)}\right]^{1/p} & a-a_0\geq t\end{cases} \tag{10.1}$$

with parameters K_0 and y_{max}.

If

$$K(s+a-t,s)=K_0+A\cos\frac{2\pi}{T}(s-t_\phi)$$

in Equation 10.0, then

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{K_0(a-a_0)+\frac{AT}{\pi}\sin\frac{\pi}{T}(a-a_0)\cos\frac{2\pi}{T}(t-t_\phi)-\frac{1}{2}(a-a_0)}\right]^{-1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{-K_0(t-t_0)-\frac{AT}{\pi}\sin\frac{\pi}{T}(t-t_\phi)\cos\frac{2\pi}{T}(t_0-t_\phi)-\frac{1}{2}(t-t_0)}\right]^{-1/p}, & a-a_0\geq t\end{cases} \tag{10.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$, if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$, if $a-a_0\geq t$ in Equation 10.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases}\left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(a_0,t-a+a_0)^{p}}\right)e^{K_{max}(a-a_0)-(K_{max}-K_{min})\alpha\left(e^{-(a-a_0)/\alpha}-1\right)}\right]^{1/p} & a-a_0<t\\ \left[\dfrac{1}{y_{\max}^{p}}-\left(\dfrac{1}{y_{\max}^{p}}-\dfrac{1}{y(t_0+a-t,t_0)^{p}}\right)e^{K_{max}(t-t_0)-(K_{max}-K_{min})\alpha\left(e^{-(t-t_0)/\alpha}-1\right)}\right]^{1/p}, & a-a_0\geq t\end{cases} \tag{10.3}$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Age- and time-dependent growth models of Gompertz (1825) type

If

$$f(y(a,t))=\lim_{p\to 0}\frac{y(a,t)}{p}\left[1-\left(\frac{y(a,t)}{y_{\max}(a,t)}\right)^{p}\right]=y(a,t)\left[\log_e\left(y_{\max}(a,t)\right)-\log_e\left(y(a,t)\right)\right],$$

Equations 1 and 2 become, respectively,

$$\frac{\partial y(a,t)}{\partial a}+\frac{\partial y(a,t)}{\partial t}=K(a,t)y(a,t)\left[\log_e\left(y_{\max}(a,t)\right)-\log_e\left(y(a,t)\right)\right] \tag{11}$$

$$\frac{dw_c(t)}{dt}=K(t+c,t)w_c(t)\left[\log_e\left(y_{\max}(t+c,t)\right)-\log_e\left(w_c(t)\right)\right]. \qquad t\geq t_c \tag{12}$$

Notice that Equation 12 can be written as a linear ordinary differential equation for $\log_e(w_c(t))$, i.e. as

$$\frac{d\log_e\left(w_c(t)\right)}{dt}=-K(t+c,t)\log_e\left(w_c(t)\right)+K(t+c,t)\log_e\left(y_{\max}(t+c,t)\right).$$

Thus, to obtain equations under the assumption corresponding to Equations 7–10.3, one can either take limits of equations 7–10.3 for $p \to 0$ or solve Equation 12 directly. I chose the latter, without resort to applying the L'Hôpital's rule to log-transformed quantities to evaluate these limits. Solution of Equation 12 as an initial value problem with $w_c(t)\,|_{t=t_c} = w_c(t_c)$ yields

$$w_c(t) = w_c(t_c)^{\,e^{\int_{t_c}^{t} K(s+c-t,s)\log\left(y_{max}(s+c-t,s)/w_c(s)\right)ds}}, \qquad t \geq t_c \tag{13}$$

If $a-a_0<t$, then $c<0$, $-c>0$, then $t_c=a_0-c=t-a+a_0$; if $a-a_0 \geq t$, then $c \geq 0$, $-c \leq 0$, then $t_c=t_0$. In other words,

$$y(a,t) = \begin{cases} y(a_0, t-a+a_0)^{\,e^{\int_{t-a+a_0}^{t} K(s-a+a_0,s)\log\left(y_{max}(s-a+a_0,s)/y(s-a+a_0,a_0)\right)ds}} & a-a_0 < t \\ y(t_0+a-t,t_0)^{\,e^{\int_{t_0}^{t} K(s-a+t_0,s)\log\left(y_{max}(s-a+t_0,s)/y(s-a+t_0,t_0)\right)ds}}, & a-a_0 \geq t \end{cases} \tag{14}$$

If $y_{max}(s+a-t,s)=y_{max}$=constant in Equation 14, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{\,e^{\int_{t-a+a_0}^{t} K(s-a+a_0,s)\,ds}} & a-a_0 < t \\ y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{\,e^{\int_{t_0}^{t} K(s-a+t_0,s)\,ds}}, & a-a_0 \geq t \end{cases} \tag{14.0}$$

If $K(s+a-t,s)=K_0$=constant in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{\,e^{K_0(t-a+a_0-t)}} & a-a_0 < t \\ y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{\,e^{K_0(t_0-t)}}, & a-a_0 \geq t \end{cases} \tag{14.1}$$

which is the age- and time-dependent Gompertz (1825) growth model, with parameters K_0 and y_{max}.

If

$$K(s+a-t,s) = K_0 + A\cos\frac{2\pi}{T}(s-t_0)$$

in Equation 14.0, then

$$y(a,t) = \begin{cases} y_{max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{max}}\right]^{\,e^{\int_{t-a+a_0}^{t} \left(K_0 + A\cos\frac{2\pi}{T}(s-t_0)\right)ds}} & a-a_0 < t \\ y_{max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{max}}\right]^{\,e^{\int_{t_0}^{t} \left(K_0 + A\cos\frac{2\pi}{T}(s-t_0)\right)ds}}, & a-a_0 \geq t \end{cases} \tag{14.2}$$

where K_0, y_{max}, A, T, and t_ϕ are model parameters to be estimated or specified.

If $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t+a-a_0)/\alpha}$ if $a-a_0<t$ and $K(s+a-t,s)=K_{max}-(K_{max}-K_{min})e^{-(s-t_0)/\alpha}$ if $a-a_0\geq t$ in Equation 14.0, then (note that $t-a+a_0-t_0=0$, or $t-t_0=a-a_0$)

$$y(a,t)=\begin{cases} y_{\max}\left[\dfrac{y(a_0,t-a+a_0)}{y_{\max}}\right]^{\left(\frac{K_{max}-K_{min}}{K_{max}-K_{min}}\right)^{\frac{a-a_0}{\alpha}}} & a-a_0<t \\ y_{\max}\left[\dfrac{y(t_0+a-t,t_0)}{y_{\max}}\right]^{\left(\frac{K_{max}-K_{min}}{K_{max}-K_{min}}\right)^{\frac{t-t_0}{\alpha}}} & a-a_0\geq t \end{cases} \tag{14.3}$$

where K_{max}, K_{min}, y_{max}, and α are model parameters to be estimated or specified.

Data requirements for parameter estimation

Equations 6, 10, and 14, and their special cases are segmented functions; they provide flexibility in the analysis of growth data. Thus, by appropriately choosing time t (which is a relative quantity), one can use either segment ($a-a_0<t$ or $a-a_0\geq t$) for an individual animal or for a group of individuals, or use both segments ($a-a_0<t$ and $a-a_0\geq t$) for a group of individuals. It is, however, more convenient to use only one segment in a single analysis. Indeed, although growth parameters can be estimated by use of either segment of any of Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3, it is easier to use the segment for $a-a_0<t$, by letting time t start before the animals, whose growth is to be modeled, are born, unless time is allowed to take negative values. Use of the other segment, i.e., that for $a-a_0\geq t$, gives identical results, but it is tortuous and requires first calculating $y(t_0+a-t,t_0)$.

Data requirement for estimation of parameters in a growth model is a function of the generality of that model: the more general it is, the more data it generally requires. Equations 6, 6.0, 10, 10.0, 14, and 14.0 generally require knowledge of two ages a_0 and a, time t, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$ if $a-a_0<t$; or knowledge of two times t_0 and t, age a, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$ if $a-a_0\geq t$.

By contrast, use of Equations 6.1, 10.1, and 14.1 only requires knowledge of the difference between two ages $a-a_0$, and two sizes $y(a_0,t-a+a_0)$ and $y(a,t)$; or of the difference between two times $t-t_0$, and two sizes $y(t_0+a-t,t_0)$ and $y(a,t)$. Equation 6.1 has been widely used to model tagging data, where a_0 or t_0 is interpreted as time at release, a or t as time at recapture, $a-a_0$ or $t-t_0$ as time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at release, and $y(a,t)$ as size at recapture. It has also been used extensively to model size at age data (obtained, say, by ageing animals by reading marks in their hard parts), where a_0 or t_0 is interpreted as age at birth, a or t as age, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ as size at birth, and $y(a,t)$ as size at age. However, it is rare to know an animal's two ages and their corresponding sizes; what are commonly measured are one age and its corresponding size. Consequently, it is common practice to fit Equation 6.1 into such size-at-age data to estimate age at birth a_0 or t_0, as well as the growth parameters, thereby implicitly assuming, for all animals concerned, that the size at birth $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$ is zero and that the age at birth a_0 or t_0 is the same. Exactly the same argument applies to Equations 6.2, 6.3, 10.1, 10.2, 10.3, 14.1, 14.2, and 14.3.

Data analysis

Barramundi *L. calcarifer* is a protandrous fish found in estuaries and other coastal areas of the Indo-West Pacific (Griffin, 1987). Between August 1977 and June 1980, 4933 barramundi with a body total-length range of about 10–100 cm were captured by a combination of lure fishing, tidal trap, seine, and gill net. They were measured to the nearest centimeter, tagged with the then commonly used, but apparently physically and physiologically damaging, Floy FT-2 dart tags for fish >35 cm and FD-67 anchor tags for fish <35 cm, and released in rivers flowing into the Van Diemen Gulf and the Gulf of Carpentaria of northern Australia (Davis and Reid, 1982). Of those tagged, 312 fish of a total length of 23–92 cm (mean=60 cm, SE=13 cm) were recaptured, but only 308 are used in the analysis below owing to incomplete recapture information. The time at liberty ranged from zero to 932 d, with a mean of 219 d (SE=211 d), and the length increment from –21 to 35 cm, with a mean of 6 cm (SE=8 cm). Negative increments in length are often observed in a tagging experiment because tagged animals can shrink in size immediately after tagging.

Let a_0 or t_0 denote time at release, a or t, time at recapture, $a-a_0$ or $t-t_0$, time at liberty, $y(a_0,t-a+a_0)$ or $y(t_0+a-t,t_0)$, the length of a fish at release, $y(a,t)$,

its length at recapture, and y_{max}, its maximum length. The segments of Equations 6.1, 10.1, 14.1; Equations 6.2 (p=1), 10.2 (p=1), 14.2 (p=1); and Equations 6.3, 10.3, 14.3, all for $a-a_0<t$, were fitted into the tagging data, by using the nonlinear least squares method, under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960 (see below for its significance), and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2 (Table 3). A likelihood ratio test suggests that Equation 6.1 is significantly different from Equation 6.2 ($F_{2,304}$=48.6892, P<0.0001) or from Equation 6.3 ($F_{2,304}$=4.1238, P=0.0171); Equation 10.1 (p=1) is significantly different from Equation 10.2 (p=1) ($F_{2,304}$=45.3460, P<0.0001) or from Equation 10.3 (p=1) ($F_{2,304}$=3.3241, P=0.0373); and Equation 14.1 is significantly different from Equation 14.2 ($F_{2,304}$=46.8516, P<0.0001) or from Equation 14.3 ($F_{2,304}$=3.5345, P=0.0304). Thus, Equations 6.2, 6.3; Equations 10.2 (p=1), 10.3 (p=1); and Equations 14.2, 14.3, and their associated estimates of parameters seem adequate for describing the tagging data. Selection between equations 6.2 and 6.3, between Equations 10.2 and 10.3, and between Equations 14.2 and 14.3 by developing more general models of $K(a,t)$ was not successful because of a lack of data.

Are equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, 14.3 independent of the start of time?

An age- and time-dependent growth model is useful, if and only if it is independent of the start of time or if it is time-homogeneous. The reason for this is that start of time is unknown. For Equations 6.0, 10.0 and 14.0 to be useful,

$$\int_{t_i}^{t} K(s+a-t,s)ds$$

if $a-a_0<t$ or

$$\int_{t_i}^{t} K(s+a-t,s)ds$$

if $a-a_0 \geq t$ must be independent of the start of time t. Obviously, Equations 6.1, 6.2, 6.3; 10.1, 10.2, 10.3; 14.1, 14.2, and 14.3 all are independent of the start of time, where time t appears as time differences $t-t_0$ or $t-t_\phi$.

However, interesting differences exist among them. Equations 6.1, 6.3, 10.1, 10.3, 14.1, and 14.3 apply on any time scales, without any adjustment of estimates of their parameters in subsequent applications because they depend on time difference $t-t_0$ or age difference $a-a_0$ only. By contrast, Equations 6.2, 10.2 and 14.2 and estimates of their parameters must be properly adjusted for this purpose. Specifically, the estimate of parameter t_ϕ in Equations 6.2, 10.2, and 14.2 must be correctly adjusted before their subsequent applications. To make such an adjustment, suppose that all growth parameters are estimated from tagging data by using one segment of Equation 6.2, 10.2, or 14.2 on one time scale (regression time scale, Fig. 1), with time t, parameter t_ϕ (estimated), and a reference time t_r (known). Now, Equation 6.2, 10.2, or 14.2 is to be applied in a future fish stock assessment on another time scale (application time scale, Fig. 1), with time t', parameter t_ϕ' (unknown,

Table 3

Estimates and (in parentheses) standard errors of parameters by fitting Equations 6.1, 6.2, 6.3; 10.1 (p=1), 10.2 (p=1), 10.3 (p=1); and 14.1, 14.2, 14.3 to the barramundi tagging data using the least squares method under the assumptions that T=365.25 d, time started (i.e. time t=0) on 1 January 1960, and errors in $y(a,t)$ follow independent normal distributions, with a mean of $\hat{y}(a,t)$ and a constant variance of σ^2. P<0.0001; n=308; — = not applicable.

Equation	v_{max} (cm)	K_0 or K_{max} (d^{-1})	A or K_{min} (d^{-1})	t_ϕ or α (d)	df_1, df_2, F	$\hat{\sigma}^2$ (cm^2)	R^2
6.1	113.4724 (9.6232)	0.00065 (0.00013)	-	—	2,306,30965.9769	22.8923	0.9951
6.2	114.4452 (8.6686)	0.00061 (0.00011)	0.00088 (0.00018)	62.7197 (06.8279)	4,304,20333.2870	17.4525	0.9963
6.3	110.1152 (8.5316)	0.00078 (0.00017)	−0.00028 (0.00121)	28.7594 (41.6473)	4,304,15801.1643	22.4343	0.9952
10.1	94.7255 (3.2775)	0.00161 (0.00014)	—	-	2,306,30895.5263	22.9443	0.9951
10.2	96.2908 (3.0613)	0.00148 (0.00012)	0.00217 (0.00028)	63.5155 (06.7582)	4,304,19947.8597	17.7884	0.9962
10.3	94.4251 (3.1934)	0.00182 (0.00020)	−0.00012 (0.00250)	37.3267 (63.1348)	4,304,15684.0774	22.6010	0.9952
14.1	100.5592 (4.8653)	0.00114 (0.00014)	—	—	2,306,31051.6220	22.8295	0.9951
14.2	102.1717 (4.5198)	0.00104 (0.00011)	0.00153 (0.00022)	63.2525 (06.7674)	4,304,20202.0707	17.5654	0.9963
14.3	99.6456 (4.6446)	0.00129 (0.00018)	−0.00028 (0.00203)	31.6268 (51.7115)	4,304,15784.7666	22.4575	0.9952

to be calculated), and a reference time t_r' (known). Both reference times must be chosen properly, such that $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale, where t_c is an arbitrarily chosen time. For example, $t_r=0$ on t_r's scale; $t_r'=0$ on t_r''s scale. Projection of both $t_r=t_c$ on t_r's scale and $t_r'=t_c$ on t_r''s scale onto a third time scale (projection time scale, Fig. 1) to find their time difference on the third time scale $\tau_r'-\tau_r$. It is this time difference that is to be used to calculate t_ϕ'. To do so, let $t_r-t_\phi=t_r'-t_\phi'$, or $t_\phi'=t_\phi+t_r'-t_r=t_\phi+\tau_r'-\tau_r$, $t-t_\phi=t'-t_\phi'=t'-t_\phi-t_r'+t_r=t'-t_\phi-\tau_r'+\tau_r$. Therefore, in Equations 6.2, 10.2, and 14.2, replacement of $t-t_\phi$ with $t'-t_\phi-\tau_r'+\tau_r$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ will give the correct growth models for the future fish stock assessment on the required time scale (application scale). For the barramundi growth described by equation 6.2, $\hat{t}_\phi$= 62.7197 d, $t_r=0$ corresponds to $\tau_r=1$ January 1960 (row 2, Table 3), $t_r'=0$ corresponds to $\tau_r'=1$ January 1999, then $t_\phi'=\hat{t}_\phi+\tau_r'-t_r=62.7197+$(1 January 1999)−(January 1, 1960)$=62.7197+14245=14307.7197$ d. Therefore, replacement of $t-t_\phi$ with $t'-14307.7197$, of $a-a_0$ with $a'-a_0'$, and of $t-t_0$ with $t'-t_0'$ in the model concerned will give the correct growth models for the future (when time starts on 1 January 1999) barramundi stock assessment on the required time scale (application scale). In this example, the third time scale (projection time scale) is, of course, calendar time.

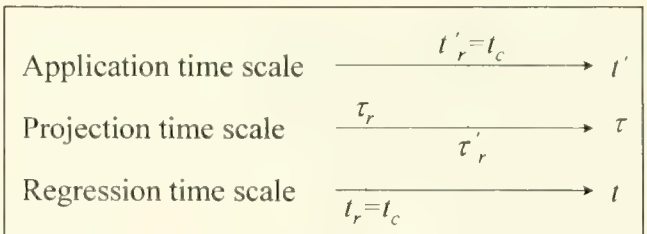

Figure 1

Relation among regression, application, and projection time scales for adjusting estimates of parameters in Equations 6.2, 10.2, and 14.2 for subsequent applications.

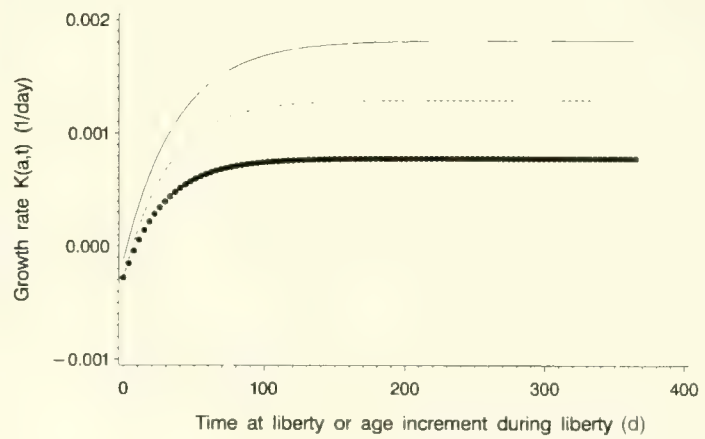

Figure 2

Growth rate $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(a-a_0)/\alpha}$ if $a-a_0<t$ and $K(a,t)=K_{max}-(K_{max}-K_{min})e^{-(t-t_0)/\alpha}$ if $a-a_0\geq t$ as a function of age difference $a-a_0$ or time difference $t-t_0$ in Equations 6.3 (•••), 10.3 (—) and 14.3 (---), with estimates of parameters K_{max}, K_{min}, and α in Table 1 for *L. calcarifer*.

Discussion

This work presents general age- and time-dependent models for the growth of animals and a comprehensive list of their useful special cases, forming a basis for obtaining quantitative information on the growth of animals experiencing changes in age, time, and age- and time-varying factors. These models have many applications. An obvious one would be to examine both the short- and long-term effects of tagging on the growth of animals by use of Equations 6.3, 10.3, and 14.3; $K_{max}<K_{min}$, $K_{max}=K_{min}$, and $K_{max}>K_{min}$ indicate, respectively, positive, no, and negative effects of tagging on the growth of animals. Similarly, $K_{min}<0$, $K_{min}=0$, and $K_{min}>0$ suggest, respectively, a shrinkage, cessation of growth, and a slower growth of tagged animals immediately after tagging. In the case of the *L. calcarifer* (Fig. 2), tagging seems to have been antagonistic to its growth ($K_{max}>K_{min}$) and led to a shrinkage of its size ($K_{min}<0$). This conclusion is tentative, however, because of the large standard error of $\hat{\alpha}$.

Another application would be to study how age- and time-dependent factors other than age and time affect the growth of animals. For example, one can hypothesize about the functional forms of $K(a,t)$, such as $K(a,t)=\alpha T(t-t_r)^\beta$, where $T(t)$ is ambient temperature, availability of food, or pH value; t_r (a time lag or lead), and α and β are all parameters to be estimated or specified. Such a model is ideal for analyzing data on the length or weight of an individual animal at age and time, which may be available, say, from aquaculture operations. It might also be useful for analyzing data from mark-recapture experiments, where ambient temperature or food availability of a tagged animal is measured continuously from the time of its tagging to the time of its recapture. Indeed, if *L. calcarifer* had been tagged with a "smart" tag that could record ambient temperature or food availability, analysis would have been made of their

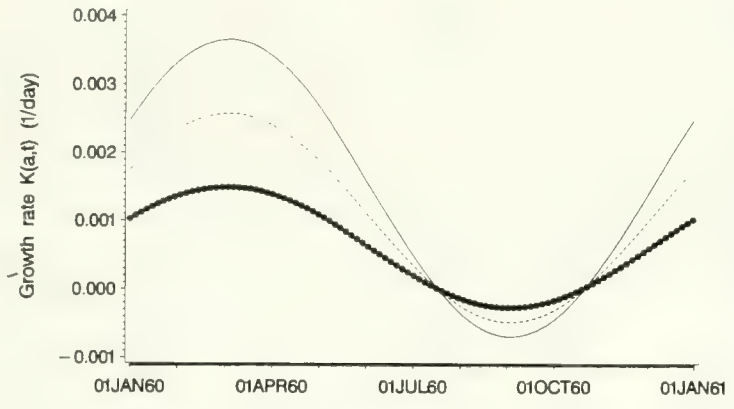

Figure 3

Growth rate $K(a,t)=K_0+A\cos\frac{2\pi}{T}(t-t_\phi)$ as a function of time t in equations 6.2 (•••), 10.2 (—) and 14.2 (---), with estimates of parameters K_0, A, and t_ϕ in Table 1 for *L. calcarifer*, and T=365.25 d.

Finally, notice my use of the length at recapture rather than length increment of a tagged individual as the independent variable in relevant models and in the data analysis. This was to avoid error propagation. The variance of the length increment is

$$V(L_2-L_1)=V(L_2)+V(L_1)-2\rho(L_1,L_2)\sqrt{V(L_1)V(L_2)},$$

where $\rho(L_1,L_2)$ is the correlation coefficient between lengths L_1 and L_2.

A higher value of noise to signal ratio is expected if length increments are used; the higher value of noise to signal ratio helps mask patterns in the data and makes their analysis difficult.

lengths at release and recapture and at times at liberty in the above application. It should be noted, however, that the information from a tagging experiment is limited. It might not be possible to estimate all the parameters in the model reliably, as in the case of the *L. calcarifer* data. Such a limitation also applies to extracting environmental signals from growth data.

More importantly, all the above models can be used to study the population dynamics of some species of animals, simply by letting $y(a,t)$ denote the number of individuals of a species of animals of age a at time t. Indeed, similar models in studies of population dynamics also lead to partial differential equations (e.g. Nisbet and Gurney, 1982).

It is interesting that *L. calcarifer* is a tropical and subtropical species of fish and yet exhibits a strong seasonal growth. For all three models (Equations 6.2, 10.2, or 14.2), its growth rate $K(a,t)$ reaches its maximum on 3 or 4 March (i.e. at the start of autumn), slows down to zero on 17 July (i.e. in the middle of winter), reaches its minimum on 2 or 3 September (i.e. at the start of spring), returns to zero on 19 or 20 October (i.e. in the middle of spring), and comes back to its maximum rate on 3 or 4 March (i.e. at the start of autumn) (Fig. 3). Thus, its length grows fastest on 3 or 4 March (i.e. at the start of autumn), grows less until a full stop on 17 July (i.e. in the middle of winter), shrinks until 19 or 20 October (i.e. in the middle of spring), and resumes a positive growth for another cycle. Thus, *L. calcarifer* does not grow in length for three months in a year, from 17 July (i.e. in the middle of winter) to 19 or 20 October (i.e. in the middle of spring). Such a strong seasonality in growth seems related to the seasonal availability of food and seasonal changes in water temperature.

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An analysis of variation in catchability of green tiger prawn, *Penaeus semisulcatus*, in waters off Kuwait

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Abstract.—A method for assessing variation in catchability of single cohort fisheries based on catch and effort statistics was developed. The results of its application to the Kuwait shrimp, *Penaeus semisulcatus*, fishery showed that catchability declined gradually with progress of fishing in general, but there was a rise in December or January. The pattern of variation was associated with possible schooling behavior at the beginning of a fishing season. Initially, catchability was high, but, as intensive fishing dispersed the schools, or reduced population density, catchability declined. The midwinter increase in catchability was probably due to an inshore spawning migration. There were also substantial interseasonal variations in catchability because schooling was associated with strong recruitment and environmental conditions.

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Most fishery management regulations are based on estimation of resource abundance and fishing mortality, of which catchability is an essential element. The existing literature on population dynamics rarely deals directly with catchability *per se*. For most production models and cohort models that use abundance indices, catchability is usually taken as constant and, subsequently, catch per unit of effort (CPUE) from commercial catch and effort statistics is used as an index of stock abundance.

The assumption of constant catchability is rarely, if ever, valid within a fishing season (Garcia, 1988; Atran and Loesch, 1995; Hannah, 1995; Arreguin-Sanchez, 1996), particularly for short-lived species such as certain shrimp in Kuwait's waters. Catchability depends on many factors: sensory capabilities, behavioral response of the target species (Penn, 1984; Wassenberg and Hill, 1990), environmental factors including temperature (Chittelborough, 1970; Morgan, 1974; Hill, 1985) and wind (Ehrich and Groger[1]), stock area, the relative distribution of fish and fishing (Winters and Wheeler, 1985; Hannah, 1995), and stock abundance (MacCall, 1976, 1990; Murphy, 1977; Csirke, 1989). Ricker (1975) stated that variation in catchability is likely to be the greatest source of error in models based on CPUE with constant catchability.

Shrimp fisheries are often managed by a minimum spawning stock strategy to prevent overfishing of stocks. Under such a strategy, CPUE during a spawning season is usually used as an index of spawning stock abundance, and fishing is closed when CPUE falls below a certain level (Penn, 1984; Morgan, 1989). If catchability is highly variable, indices of spawning stocks and the underlying stock recruitment relationship could be obscured and perhaps lead to erroneous management decisions (Hannah, 1995).

Studies on catchability are essential for relating stock abundance to observed CPUE. By investigating within-season changes in catchability, properties of a stock that are not apparent when only annual data are examined, can be understood better. The objective of this paper is to develop a method to estimate changes in catchability from commercial catch and effort data.

Materials and methods

The model

The *Penaeus semisulcatus* fishery in waters off Kuwait has a single major recruitment in June and July,

[1] Ehrich, S., and D. Groger. 1989. Diurnal variation in catchability of several fish species in the North Sea. ICES Council Meeting (CM) 1989/B:35, 10 p.

which, depending on the year, may be supplemented by a second, late-summer recruitment in August or early September (Mohammed et al., 1996). The success of the second recruitment was responsible for record landings, for example, in the 1988–89 and 1989–90 seasons (Siddeek et al., 1994). Total landings of *P. semisulcatus* in 1994–95 and 1995–96 were 699.7 and 925.0 tonnes, respectively, about 14% and 19% of the 1988–89 season's *P. semisulcatus* catch of 5022.4 tonnes (Siddeek et al., 1994).

Kuwait's opening date for shrimping has been set at 1 September since 1987 (Gulland, 1989; Siddeek and Abdul-Ghaffar, 1989). The season is closed when the CPUE for combined species of the industrial fleet falls below 80–120 kg/boat-day (Xu et al., 1995). In this case, shrimp trawling is a process that depletes a single cohort.

We start with three basic equations. The first equation is the relation between fishing mortality and fishing effort:

$$F_t = q_j f_t, \tag{1}$$

where q_j = catchability in month j;
F_t = fishing mortality in time interval t (5 days per interval); and
f_t = fishing effort in time interval t.

The second relates the population number at time t to the initial cohort number and cumulative fishing and natural mortalities:

$$N_t = Re^{-\sum_{i}^{t} F_i - tM}, \tag{2}$$

where R = initial stock number;
N_t = population number at time t;
i = time interval; and
M = natural mortality.

The final equation relates catch to current abundance and fishing as well as to natural mortalities, and we assume that fishing mortality acts independently of natural mortality, taking a fraction of $F/(F+M)$ of the total mortality, so

$$C_t = N_t \frac{F}{F_t + M}\left(1 - e^{-(F_t + M)}\right), \tag{3}$$

where C_t = catch in time interval t.

The three equations describe an exponential decay process of a single cohort with fishing and natural mortalitites. Natural morality is assumed to be independent of time throughout the season and catchability is assumed to remain constant within a month.

Given catch and effort data, the initial population number (R), natural mortality rate (M), and six monthly catchability rates (q_j), a total of eight parameters can be estimated in theory by a time-series fitting method of least squares between observed and predicted catches. There exists, however, a problem of confounding the initial stock number, natural mortality, and catchabilities. A high initial population number with high natural mortality and low catchability rates gives as good a fit as does a low initial population number with a low natural mortality and high catchability rates. The following three measures were taken to solve this problem.

1) We assumed that

$$R = \frac{1}{q_1}\sum_{t=1}^{3} C_t' \Big/ \sum_{t=1}^{3} f_t, \tag{4}$$

where C_t' = observed catch at time t.

This assumption says, in effect, that for a given estimate of q_1, we have an estimate of the initial population number (R) from the average catch and effort over the first three time intervals (Hilborn and Walters, 1992). 2) It was presumed that natural mortality was available from other sources. 3) Auxiliary abundance index was used in the time series fitting as follows:

$$SS = \sum_{t=1}^{T}\left[\ln(C_t) - \ln(C_t')\right]^2 + W\sum_{j=1}^{J}\left[\ln(X_j) - \ln(X_j')\right]^2, \tag{5}$$

where C_t = predicted catch at time t by Equation 3;
C_t' = observed catch at time t;
X_j' = observed index of stock number in month j in relation to the beginning point of a fishing season;
X_j = predicted relative stock abundance in the middle of month j, i.e. predicted stock number in month j divided by the predicted stock number of the middle point of the beginning month; and
W = the weight given to the deviation between the predicted and the observed stock indices.

This procedure reduced the number of parameters to be estimated to six. Monthly CPUE of the United Fisheries of Kuwait (UFK) fleet was used as auxiliary information about stock abundance.

The data

The shrimp fishery in Kuwait consists of two sectors: industrial trawlers and dhow trawlers (for a review see Mathews and Samuel, 1991; Mathews, 1994; Ye et al., 1996). The main species caught are *P. semisulcatus*, *Metapenaeus affinis*, and *Parapenaeopsis stylifera*. *Penaeus semisulcatus* dominates in the central and southern waters, and the other two species are mainly distributed in northern waters. The dhow boats trawl in relatively shallow waters, and their catches are auctioned at local fish markets (Abdul-Ghaffar and Al-Ghunaim, 1994; Ye et al., 1996). Species composition of the dhow catch varies with changes in fishing grounds and with seasonal migration. The monthly percentages of *P. semisulcatus* in the dhow landings change greatly within a season, for example, from 29.6 to 87.1% in 1993–94. Owing to the difficulty in collecting reliable effort data from the dhow sector, effort is usually standardized in relation to that of the industrial sector in reporting Kuwait's shrimp fishery statistics. The dhow effort is thus calculated by dividing the total catch of combined species of the dhow sector by the CPUE of combined species from the industry sector (Mathews, 1994), which ignores the change in target species. The catchability of *P. semisulcatus* under such a standardized effort would change simply because of the variation in target species.

The industry sector comprises three companies: United Fisheries of Kuwait (UFK), Bubiyan Fishing Company, and National Fishing Company. The shrimp catch landed by UFK is mainly exported. Fishing operations of the UFK fleet are mainly in the southern and central Kuwait waters, where *P. semisulcatus* dominates (Siddeek et al., 1989); this occurs because *P. semisulcatus* is individually larger and much more valuable in international markets than the other two species (Siddeek et al., 1989; Ye et al., 1996). Consequently, the percentage of *P. semisulcatus* in the UFK catch remains relatively less variable within a season, for example between 59.5% and 84.5% in the 1993–94 season (Ye et al., 1996).

Seasonal landing data from the dhow boats were recorded every five days (Mohammed et al., 1996); however, industrial fleets reported their catches and fishing effort monthly. To estimate monthly variations in catchability, we assumed a uniform distribution of the industrial catch within any month and added this to dhow catches for that month. This obscured the within-month variation in catch. The dhow landings constituted about 53% of the total *P. semisulcatus* landings in the 1994–95 and 1995–96 seasons (Ye et al., 1996); therefore such an assumption would not affect the estimates of monthly catchability significantly. In our study, catchability was assumed to be constant within a month, and the fishing effort data of the *P. semisulcatus* fishery were standardized by using the entire industrial shrimping fleet catch rates, as is customary (Gulland, 1983; Mohammed et al., 1996). The total catch, fishing effort, and abundance index are shown in Table 1.

Table 1

Time series catch, effort, and relative abundance index data of the Kuwait *P. semisulcatus* fishery in the 1994–95 and 1995–96 seasons.

	Catch (10^3number)		Effort (boat-day)		Abundance index	
Time	1994	1995	1994	1995	1994	1995
5 Sep	2007	3752	266.2	357.7		
10 Sep	2212	3165	316.3	325.4		
15 Sep	1565	3201	239.9	352.8	1.000	1.000
20 Sep	1592	4502	260.0	528.8		
25 Sep	1704	1868	295.0	232.5		
30/Sep	1549	1805	282.9	237.1		
5 Oct	1589	1707	490.8	386.0		
10 Oct	782	1342	252.5	316.8		
15 Oct	925	1126	310.9	276.5	0.621	0.613
20 Oct	921	1397	321.1	356.3		
25 Oct	914	1354	329.3	356.9		
30 Oct	724	1051	268.8	285.1		
4 Nov	421	42	199.7	210.6		
9 Nov	396	331	192.0	151.5		
14 Nov	337	411	167.3	191.9	0.500	0.383
19 Nov	287	486	145.4	231.5		
24 Nov	292	404	150.0	195.8		
29 Nov	239	398	124.7	195.7		
4 Dec	460	424	211.5	398.2		
9 Dec	371	369	172.9	350.3		
14 Dec	448	409	210.7	392.1	0.574	0.202
19 Dec	496	311	235.4	301.1		
24 Dec	354	268	169.3	260.6		
29 Dec	703	395	337.8	387.6		
3 Jan	487	383	588.1	378.4		
8 Jan	260	243	315.3	240.9		
13 Jan	347	482	422.3	478.8	0.229	0.201
18 Jan	339	397	413.3	395.0		
23 Jan	339	285	413.6	283.6		
28 Jan	346	272	423.3	271.2		
3 Feb	233	93	529.9	330.2		
8 Feb	45	204	102.3	726.8	0.123	0.057
13 Feb	177	219	402.8	782.2		

Catchability by the UFK fleet is relatively stable within a fishing season. From Equations 1 and 3, $CPUE \cong qN$. CPUE can be an indicator of variation in stock abundance only when catchability q is constant. Figure 1 shows q estimates calculated by simply dividing UFK CPUE data (Siddeek et al., 1989) by the shrimp stock abundance, represented by catch

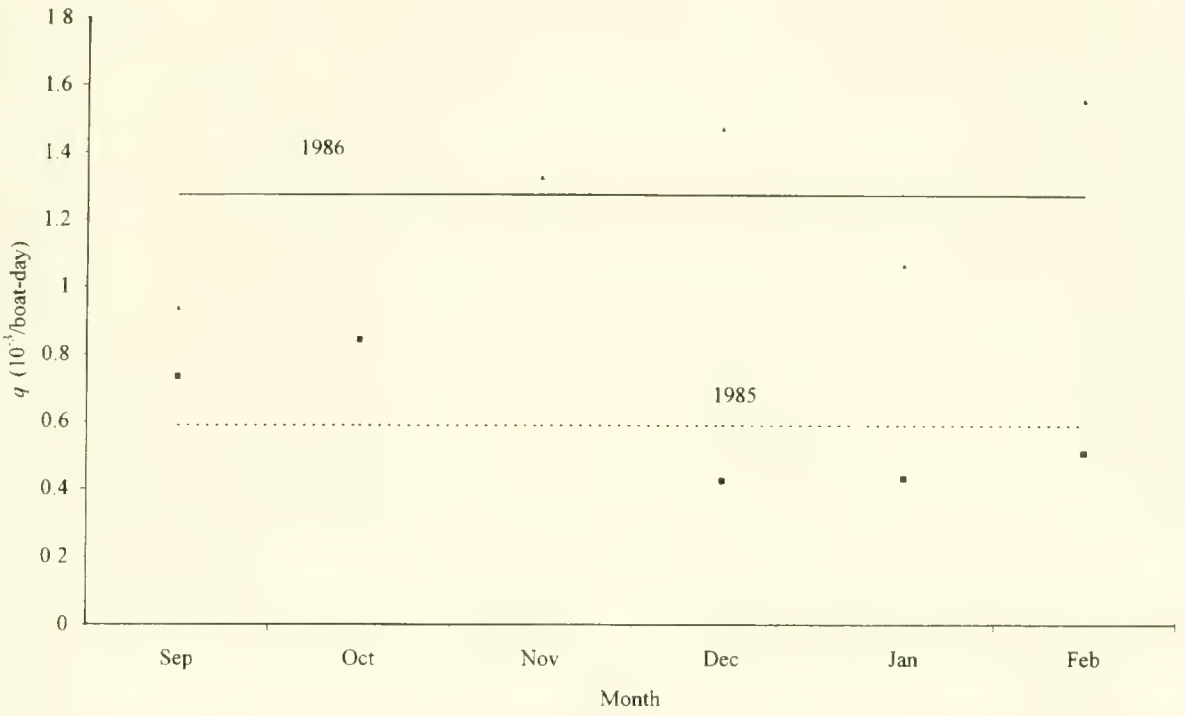

Figure 1

The catchability estimates of the UFK fleet in 1985 (■) and 1986 (▲). The survey catch rates in November 1985 and October 1986 were missing because the whole data set of five year-round surveys was destroyed during the Iraqi occupation in 1991.

rate (kg per haul of 45 minutes) of a survey vessel in 1985 and 1986. There are no survey catch rates in number available, but using catch rate in weight would not introduce any great bias in the investigation of catchability here. The catchability, q, is relatively stable within the period of the investigation, although a great difference can be seen between 1985 and 1986. Therefore, the UFK CPUE was used as an index of stock abundance of *P. semisulcatus* within a fishing season in our study.

Results

Natural mortality is supposed to be known and independent of time within a fishing season, which may violate reality, but this is a more conservative assumption than assuming that natural mortality is constant over periods of years (Hannah, 1995). The natural mortality rate of Kuwait's *P. semisulcatus* has been investigated by a number of authors (Mathews et al., 1987; Siddeek et al., 1989; Xu et al., 1995; Mohammed et al., 1996; FAO[2]; Al-Hossaini[3]); these results range from 1.8 to 4.0/yr. In this study, we used the minimum, median, and maximum estimates of natural mortality rates for our estimation of catchability.

The fits of the above developed depletion model to catch data are shown in Figure 2, in which we used a median natural mortality rate (M=2.9/yr) and produced 95% confidence intervals by the parametric bootstrap (BC) method (Efron and Tibshirani, 1986). The predicted catches for the 1994–95 and 1995–96 seasons are very close to the observed values in general. There is relatively greater discrepancy at the beginning of the seasons, however. The predicted catches are lower than the observed ones in the first month for both seasons (Fig. 2). This is caused by the assumption of Equation 4.

The calculated stock abundance indices also followed the pattern of observed population indices (Fig. 3), showing an exponential depletion of a single co-

[2] FAO (Food and Agriculture Organization of the United Nations). 1982. Assessment of the shrimp stocks of the west coast of the Gulf between Iran and the Arabian Peninsula. Food and Agriculture Organization. FAO Rep. FI:DP/RbyAB/80/015, Rome, Italy, 162 p.

[3] Al-Hossaini, M. 1993. Finfish fisheries and shrimp fisheries management. Tech. Rep., Kuwait Institute for Scientific Research. Food-4 KISR 4367, 53 p.

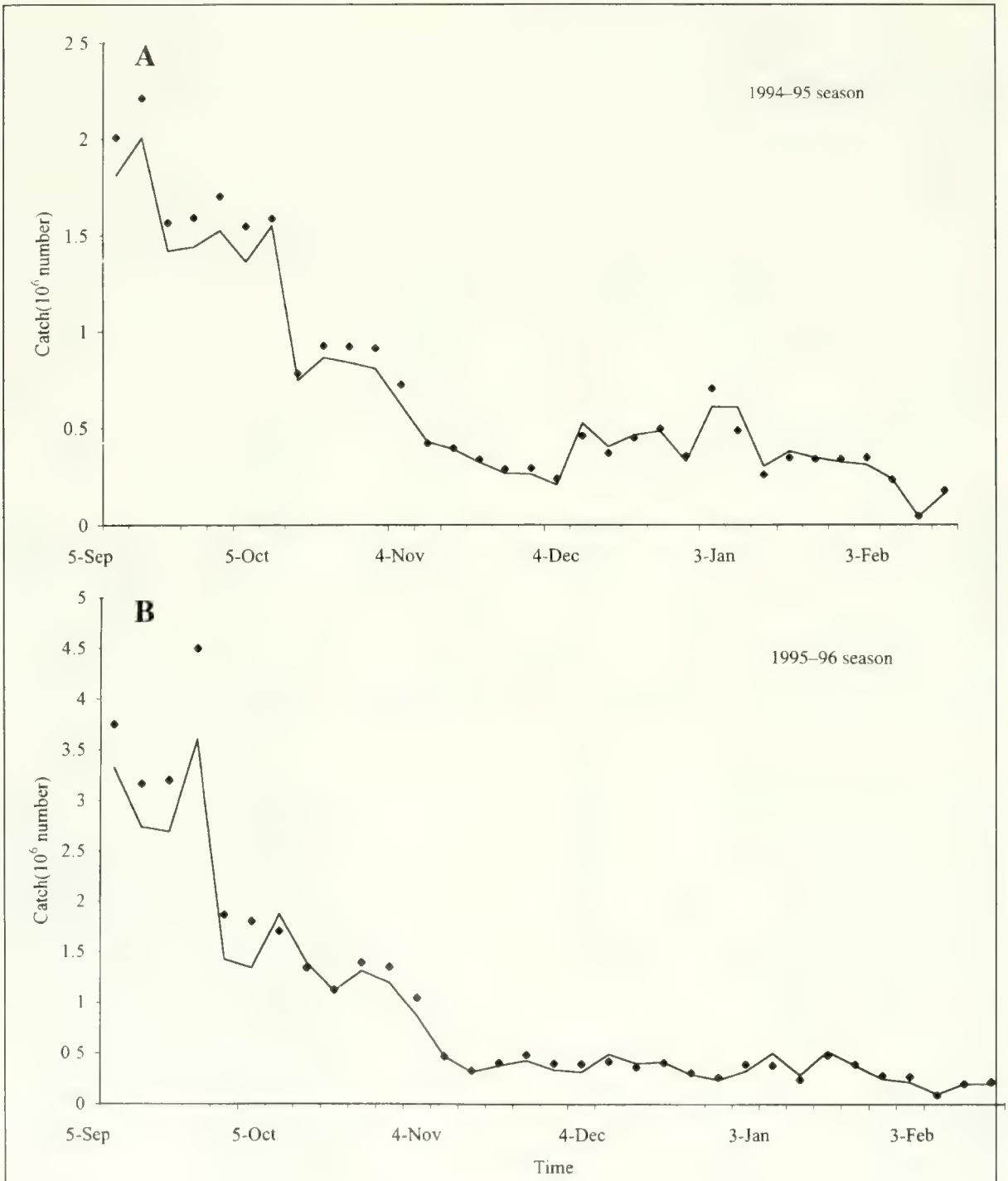

Figure 2

The fit of the model to the catch data (◆ observed data, - fit) for Kuwait's 1994–95 and 1995–96 shrimp landings from 1 September to 15 February.

hort stock. The model fit for the 1995–96 season was better than that for the 1994–95 season. A comparison of these two fits of stock abundance indices showed that the stock experienced a greater decline during the1995–96 season. Figures 2 and 3 demonstrate the goodness of the model fit.

The monthly estimates of catchability in the 1994–95 and 1995–96 seasons exhibit a declining trend as

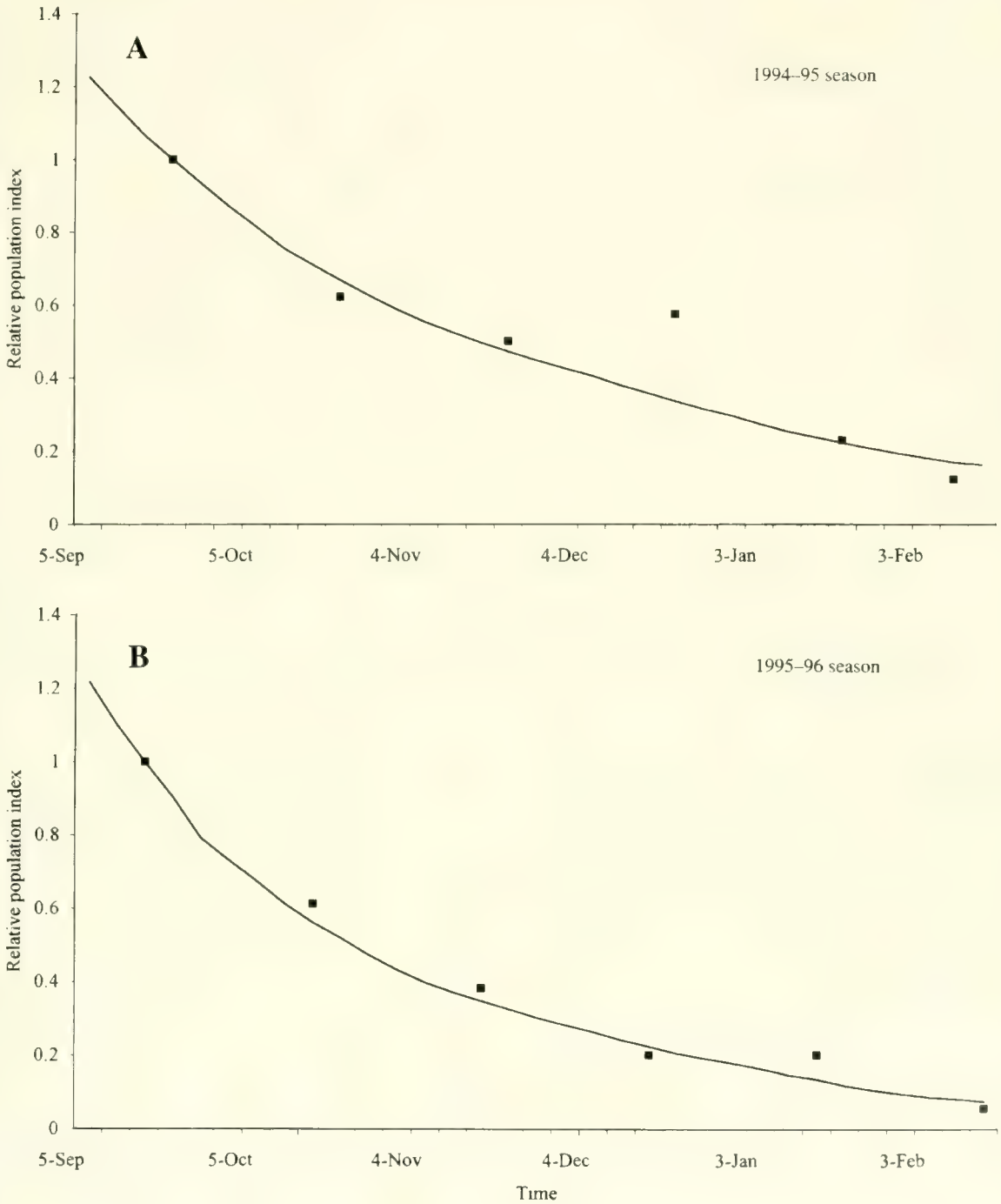

Figure 3

The fit of the model to the relative stock abundance indices (◆ observed data, - fit) for the 1994–95 and 1995–96 seasons.

the season progressed (Fig. 4). From season opening to closing, catchability decreased from 10.40×10^{-5}/boat-day to 4.63×10^{-5}/boat-day in 1994–95, and 17.05×10^{-4}/boat-day to 7.77×10^{-5}/boat-day in 1995–96, respectively (Fig. 4). Comparison between these two seasons shows that shrimp catchability at the beginning of the 1994–95 season was only about 60% of the catchability at the start of the 1995–96 sea-

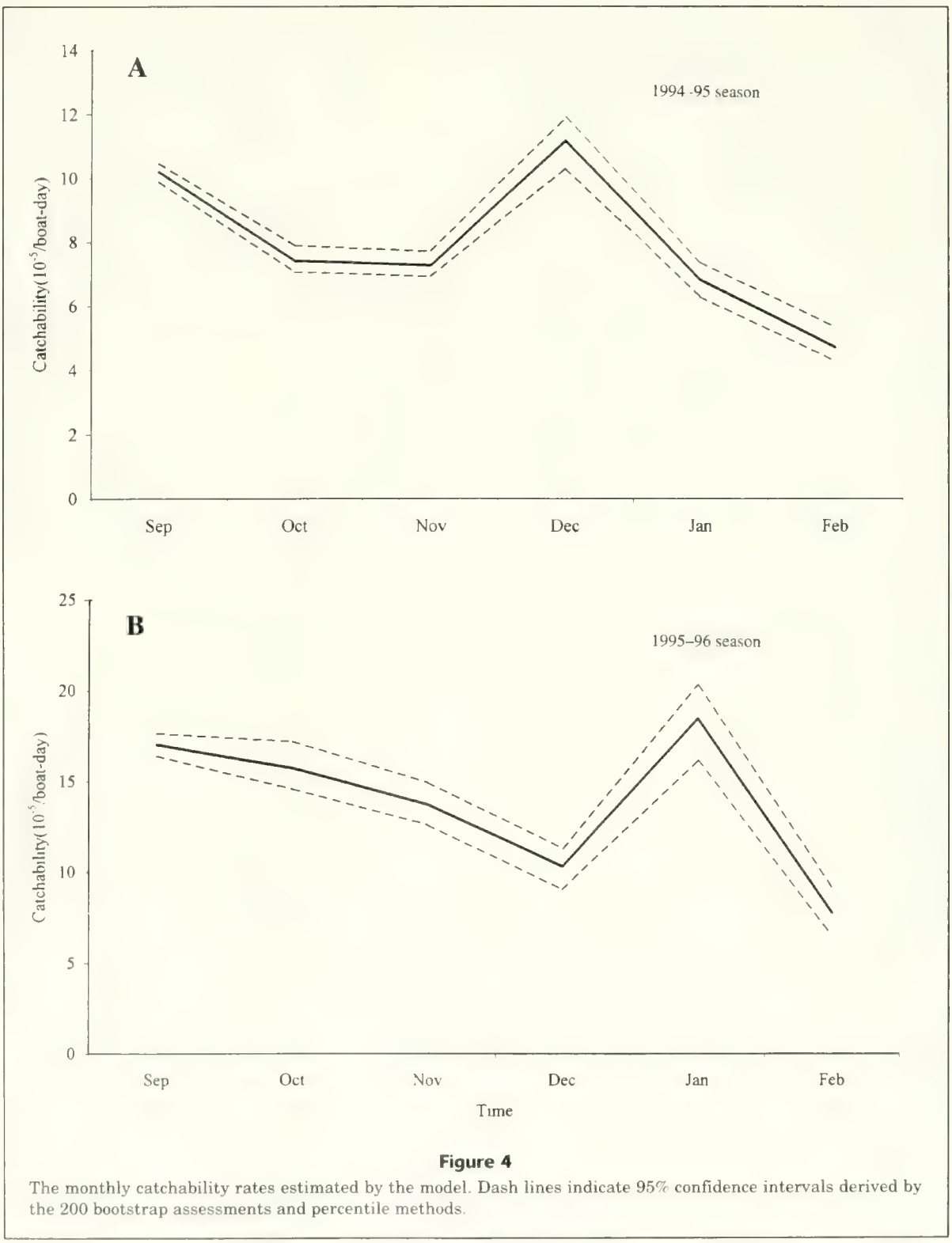

Figure 4

The monthly catchability rates estimated by the model. Dash lines indicate 95% confidence intervals derived by the 200 bootstrap assessments and percentile methods.

son. The estimates of catchability at the end of these two seasons exhibited a similar difference. The catches at the beginning of the 1995–96 season were much higher than those in the same period of the 1994–95 season (Fig. 2). High catchability rates may be associated with abundant stocks. Thus, it can be concluded that high catchability is expected when recruitment is good.

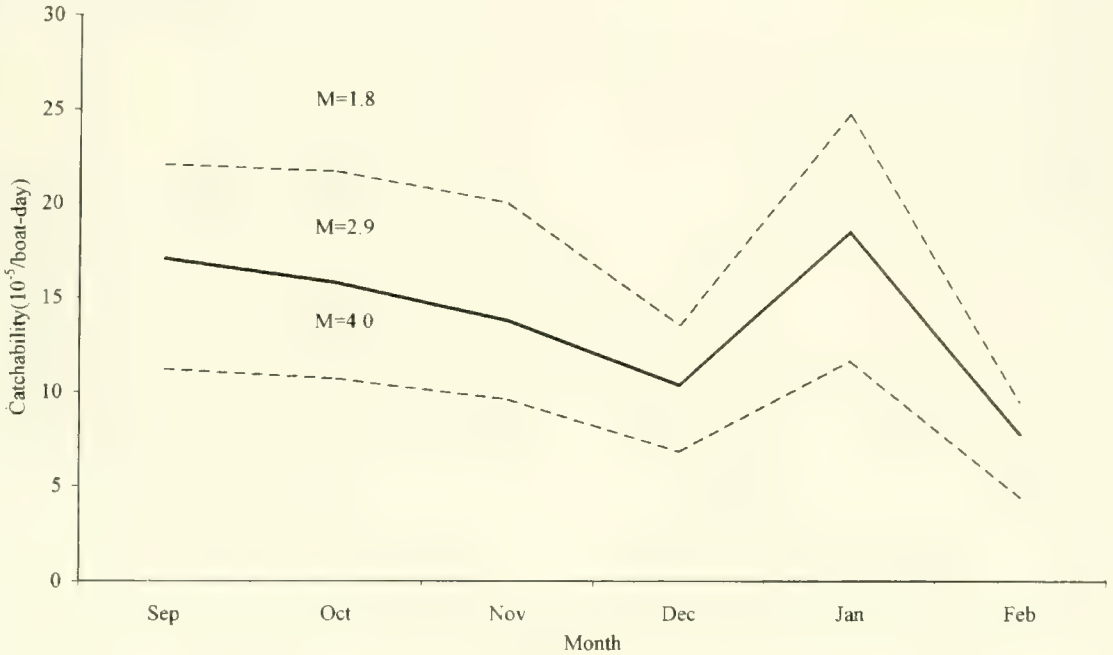

Figure 5

The effect of natural mortality on the estimation of catchability derived from Kuwait's 1995–96 season data.

Another interesting point is that there was a rise in catchability in December for the 1994–95 season, in January for the 1995–96 season. The second catchability rate peak was even slightly higher than the first one in both seasons. All these results show that catchability in the *P. semisulcatus* fishery varies within a fishing season and from year to year, but that the variation patterns in different seasons are similar, with two peaks (Fig. 4).

There are many biases in the estimation of natural morality (Vetter, 1988). The natural mortality rate used in this analysis was the median value of estimates from various sources. Different values of natural mortality will result in different estimates of catchability. Figure 5 shows comparison of the results derived from the seasonal 1995–96 data when the minimum (M=1.8/yr), median (M=2.9/yr), and maximum (M=4.0/yr) estimates of natural mortality were used. The variation of the pattern of catchability was similar within this range of natural mortality. A lower natural morality results in higher catchabilities and a relatively large variation in catchability within a fishing season, demonstrating the correlation between natural mortality and catchability. Therefore, we suggest that the variation pattern derived by this method is reliable, although absolute values may be biased by the natural mortality used.

The weight, W in Equation 5, can be assigned a high or low value depending on the reliability of the auxiliary information compared with the catch data (Hilborn and Walters, 1992). Here, we set W to 6 simply because there were six points of catch and effort data each month, but the auxiliary index had only a single datum point each month. Actually, the auxiliary information was used to constrain the predicted stock's declining track, and thus control total mortality within a certain level. A sensitivity analysis showed that reducing W by 50% resulted in an average decrease of 3.5% in catchability, ranging from 2.1% to 4.8%; increasing W by 50% leads to an increase in catchability of 7.4% on average, with a range of 5.3% to 9.6% (Fig. 6). The primary concern here is the pattern of catchability variation; it is not sensitive to the weighting factor in the case of Kuwait's *P. semisulcatus* fishery (Fig. 6). One method to determine a suitable value for W is by comparing the geometric fits of both the catch and abundance index in the case of unknown reliability over either set of data.

Discussion

An analytical framework to estimate changes in catchability of single cohort fisheries has been pro-

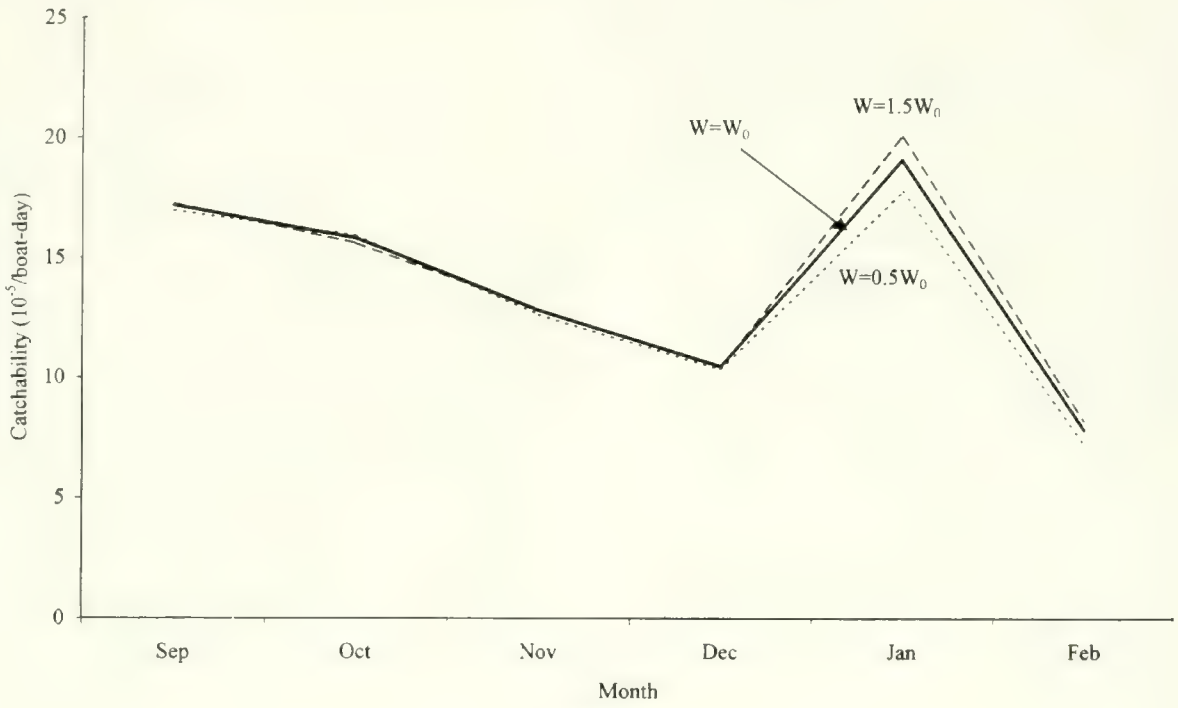

Figure 6

The effect of weighting fact, *W*, on the estimation of catchability for the 1995–96 season.

vided. The results of our study show that the catchability of the Kuwait shrimp fishery is not constant; there were high values at the beginning of the fishing season, lowest values at the end. The two-peak pattern of catchability may be associated with schooling behavior at the time of recruitment to the fishery and the spawning migration of the species. There is also great variation in catchability on an interannual basis because schooling is associated with high recruitment (Mathews et al., 1994) and certain environmental conditions (Penn, 1984).

The general declining trend in catchability may be attributed to schooling behavior. As fishing progressed, shrimp schools were depleted or dispersed, and catchability declined (Drobisheva and Aseev, 1976; Garcia and Reste, 1981; van Zalinge, 1984; Mathews et al., 1994). Reduced activity caused by low temperature is another identified cause for the decline of catchability of Spencer Gulf prawns (*Penaeus latisulcatus*) in Australia during the winter months (June to August) (Sluczanowski, 1984) and *P. semisulcatus* in Kuwait (Mathews and Al-Hossaini, 1982). Both schooling and effects of decreasing temperature likely contributed to the variation of catchability in the Kuwait shrimp fishery.

The major spawning season for *P. semisulcatus* is from December to April (Drobisheva and Aseev, 1976; Siddeek et al., 1989). Many penaeids undertake a short shoreward migration before spawning (Garcia, 1988; Ye, 1984). *Penaeus semisulcatus* in the Gulf of Carpentaria migrate from offshore into shallow waters in the spring before spawning (Dall et al., 1990). Drobisheva and Aseev (1976) reported that *P. semisulcatus* in the Arabian Gulf forms prespawning schools or aggregations in the spawning area. Although the migration pattern of *P. semisulcatus* in watters off Kuwait is still not clear, the pattern of catchability strongly indicates that this species may return to Kuwait waters before spawning season and concentrate in certain areas. Such shoreward movement by spawning schools resulted in the highest catchability, and a peak in December or January (Fig. 4), which rapidly decreased as fishing progressed.

There is also the possibility that shrimp of non-Kuwait origin migrate to Kuwait waters. El-Musa (1982) analyzed mark-recapture data and concluded that the *P. semisulcatus* released in February 1979 at Dohat Al-Zaur, close to the border with Saudi Arabia, exhibited a strong northward movement. The timing of such a migration could be affected significantly by environmental conditions associated with a spawning migration, resulting in an apparent increase in catchability earlier in some years than in others.

The schooling behavior of *P. semisulcatus* was associated with years of higher catches (van Zalinge, 1984; Mathews et al., 1994). When recruitment to the fishery was good, larger schools, and thus higher catchability, could be expected. The catches at the beginning of the 1995–96 season were much higher than those of the same period in the 1994–95 season (Fig. 2); catchability in 1995–96 was also much higher (Fig. 4). With intensive fishing effort, the shrimp stock was reduced to a very low level by the end of the fishing season, despite its initial abundance. Therefore, catchability is associated with stock abundance.

Although the variation in total mortality and catch cannot be explained by variation in natural mortality, violation of the assumption that natural mortality remains constant within a season may still be the source for biases in the estimation of monthly catchability. The relatively larger discrepancy between predicted and observed catches, the predicted being always lower than the observed, in the first month (Fig. 2) may result from a departure from the natural mortality rate that is generally used. An inflated natural mortality for the first month will give lower predicted catches because the first month's catchability was related to the initial population number, which in turn was connected to all the other estimates of catchability in the fitting scheme used in this study. The fit cannot be improved by adjusting catchability for the first month. Although it may be true that natural mortality is constant during a fishing season, a possible second recruitment in early September, which was not considered in our study and is probably rather weak, may compensate natural death to some extent and lead to a lower net natural mortality than the value we used.

This study reports apparent changes in catchability of Kuwait's *P. semisulcatus* fishery. It should be noted that M, q, CPUE, and schooling must be interrelated to a certain extent. Schooling may bias CPUE with respect to years in which it does not occur, and M estimates from any method applied in Kuwait may also be influenced if schooling occurs only in certain seasons. Changes in catchability to a fishery may be associated with both fishing power and population characteristics. A better understanding of the mechanisms underlying these results will improve stock assessment. The variations in catchability suggest that changes in catch-rate indices may not actually reflect variations in abundance. Although other results support the conclusion of this study, functional relationships among catchability and population characteristics, fleet characteristics, and environmental conditions should be studied further.

Acknowledgments

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Straying of adult sockeye salmon, *Oncorhynchus nerka*, entering a non-natal hatchery

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Salmonid fishes tend to return to their natal site ("home") for reproduction (topic reviewed by Quinn and Dittman, 1992; Quinn, 1993). Odors learned by juveniles during freshwater residence and downstream migration guide adults during the final stages of homing migration (Hasler and Scholz, 1983; Dittman and Quinn, 1996), although adults also respond to spawning site characteristics (Blair and Quinn, 1991) and odors of conspecifics (Newcombe and Hartman, 1973; Honda, 1982; Groot et al., 1986). However, some salmonids do not return to their natal site, but instead "stray" and spawn elsewhere (Quinn, 1993).

The terms "homing" and "straying" are defined by the endpoints of migration (i.e. the natal or non-natal site, respectively), but during their migration some salmonids ascend one stream, only to later leave and spawn elsewhere (Ricker and Robertson, 1935; Ricker, 1972). Mature salmonids respond to the stimulus of imprinted odors with positive rheotaxis and move downstream when they no longer detect home odors (Johnsen and Hasler, 1980); therefore movement up a non-natal stream does not necessarily mean that the fish will spawn there. It may be natural for salmon migrating up complex river systems to ascend non-natal streams for a brief distance before the absence of homestream odors triggers negative rheotaxis. However, the behavior of some fish is not adequately explained by such "proving" behavior. For example, 16% of the sockeye salmon (*Oncorhynchus nerka*) radio-tagged by Burger et al. (1995) in Tustumena Lake that eventually spawned in a particular tributary, initially entered a different tributary and stayed there for up to one week. In addition, 21% of the fish that spawned on the shoreline of the lake had previously entered a tributary stream. These fish might be "exploring" (actively seeking different sites and comparing their attributes) or "wandering" (searching in the absence of stimuli).

Unfortunately, the principal methods for studying homing fail to distinguish straying from exploring or other related behavior patterns. One approach is to collect adult salmon from spawning grounds, displace them to another spawning site or to a nonspawning area, and monitor their subsequent movements. Most of the fish returned to the site of their capture (e.g. Hartman and Raleigh, 1964; McCart, 1970; Varnavskiy and Varnavskiy, 1985; Blair and Quinn, 1991), and the authors assumed but did not verify that the capture site was home. Another approach is to capture and track adults as they move upstream to their spawning site (e.g. Berman and Quinn, 1991; Burger et al., 1995). In these studies, the final spawning location is assumed to be the natal one but this also is not verified.

The primary alternative approach to capturing and marking adult salmon is to mark them as juveniles and monitor the locations where they subsequently spawn (e.g. Quinn and Fresh, 1984; Quinn et al., 1991; Pascual and Quinn, 1994; Vander Haegen and Doty, 1995). The origin of these salmon is known, but once they enter a hatchery, they cannot leave and are only identified as strays after they are killed. Much of what we know about the frequency of straying is based on data from hatchery populations, but these data reveal little about the processes of homing and straying and may not represent wild populations (Quinn, 1993). Information on the extent to which salmon that enter a non-natal hatchery would leave, if given the opportunity, would provide insights into migratory behavior and the potential biases of estimating the extent of straying from hatchery populations.

The University of Washington hatchery (UWH) provides an excellent opportunity to study homing, exploring, and straying of salmon. The UWH releases chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon smolts each spring. Sockeye salmon are abundant elsewhere in the Lake Washington watershed, and a few enter the UWH although they are not reared there. In our study, all adult sockeye that entered the UWH were tagged and released just outside the hatchery. If they were proving or exploring, we would not expect them to re-enter the UWH. However, if they returned repeatedly after release, it would indicate that they would

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Fish. Bull. 97:713–716 (1999).

probably spawn at this non-natal site. We also tagged and released chinook salmon to compare the behavior of salmon that originated elsewhere (the sockeye) with that of salmon that presumably originated from the hatchery (the chinook).

Methods

The UWH is located approximately 10 km from Puget Sound, Washington, on the north side of Portage Bay, in the Lake Washington system (Fig. 1). It produces chinook and coho but not sockeye salmon. However, an average of eight sockeye salmon (range 4–18) entered the pond each fall during the years of this study (1992–97). Over this period, the Lake Washington system has had a mean total sockeye escapement of 175,893 (range 122,415–400,000).[1] The main spawning areas within the watershed are the Cedar River, Issaquah Creek, and Bear Creek, and all sockeye salmon spawn in the watershed upstream from the UWH outfall (Fig. 1; Hendry et al., 1996), principally in October and November.

During the years of our study, an average of 1299 chinook salmon (range 458–2229) entered the UWH, principally from early October through mid-November. Analysis of coded wire tagging (CWT) data has revealed a very high fidelity of UW salmon for the hatchery, and very low levels of straying of non-natal chinook salmon into the UWH (>>99% of the fish entering the hatchery had been released from it; Quinn and Dittman, 1992). We therefore assumed that chinook salmon entering the hatchery had been produced there but a few might have been produced elsewhere.

Twice each week during the fall, the UWH pond was partially drained and all the salmon were seined into a small area. All sockeye salmon and a subsample of the chinook salmon (in 1994–96) were transferred from the seine to a live box in the pond. These fish were tagged with a T-bar tag on each side in the musculature just below the dorsal fin and quickly released within 10 m of the ladder leading into the hatchery. All tagged chinook salmon were males (1 year olds in 1994; 2 year olds in 1995 and 1996) and releases were spread throughout the course of the run. Returning tagged fish of both species were recaptured during the seining of the pond. Those in good condition were released once more outside the hatchery but those with extensive fungus on their bodies were sacrificed. Fish that returned a third time were killed, regardless of their condition.

[1] Egan, R. 1998. Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501. Personal commun.

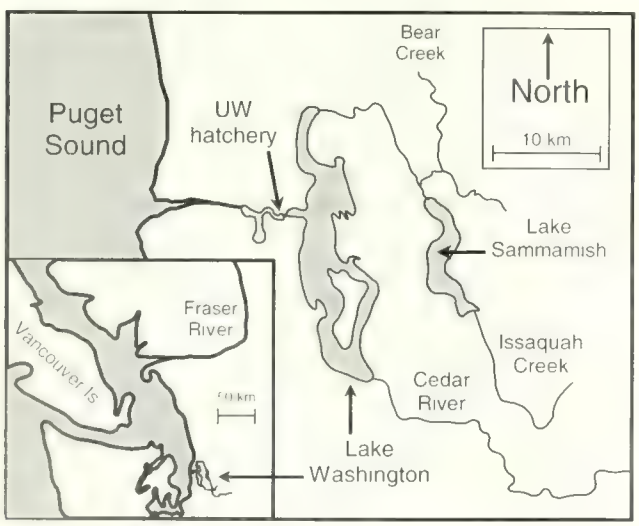

Figure 1

Map of the Lake Washington drainage, showing locations of the University of Washington (UW) hatchery and the major tributaries used by spawning sockeye salmon. Insert indicates the drainage's location in northwest Washington.

Results

Between 1992 and 1997, 48 sockeye salmon (28 males and 20 females) entered the UW hatchery and were tagged and released (Table 1). The percentage of these fish that returned to the hatchery varied from 0% to 37.5% among years with an overall mean of 20.8% (Table 1). Of the ten sockeye salmon that returned after their first displacement and that were displaced a second time, five (50%) returned again. The sex ratio of the sockeye salmon straying into the hatchery (58% males) was similar to that of those returning after displacement (60% males).

From 1994 to 1996, 132 male chinook salmon were tagged and released from the UWH (Table 1). The proportion of chinook salmon that returned after displacement did not differ among the three years (χ^2=0.015, 2 df, P>0.99, overall mean=77%, Table 1). The percentage of sockeye salmon returning after displacement was much smaller than that of the chinook salmon (20.8% vs. 77.3%; χ^2=48.5, 1 df, P<0.005). Of the chinook salmon that returned after release, 65% returned a second time.

Discussion

Our finding that most of the sockeye entering the UWH appeared to be proving or exploring rather than

Table 1

Number of adult sockeye and chinook salmon tagged and released from the University of Washington hatchery (1992–97) and numbers returning to the hatchery once and twice. Numbers in parentheses represent percentages of returning fish: percentages of those returning once are based on the total number released; percentages of those returning twice are based on the number returning once.

Species	Year	Number tagged	Numbers of fish returning	
			Once	Twice
Sockeye	1992	4	0 (0)	0 (0)
	1993	6	1 (16.7)	0 (0)
	1994	8	1 (12.5)	0 (0)
	1995	4	1 (25.0)	1 (100)
	1996	18	4 (22.2)	4 (100)
	1997	8	3 (37.5)	0 (0)
	Total	48	10 (20.8)	5 (50.0)
Chinook	1994	32	25 (78.1)	13 (52.0)
	1995	39	30 (76.9)	17 (56.7)
	1996	61	47 (77.0)	36 (76.5)
	Total	132	102 (77.2)	66 (64.7)

straying in the true sense is helpful in interpreting the movements of salmon during the final stages of their homing migration. Most of the sockeye (38 of 48) that entered the UWH and were released did not return again. From our data we cannot determine which term (proving, exploring, or wandering) best describes their behavior. However, five out of ten of the sockeye that returned once returned a second time after displacement. We do not understand the motivation for the behavior of these fish but interpret their persistence as evidence that they would have spawned at the site and thus were considered strays in the true sense.

Why did only 10 of 48 sockeye salmon re-enter the UWH? Were the others unable to locate the hatchery or did they die prior to re-entry? The proportion of chinook salmon returning to the UWH after displacement (77%) was much higher than that of sockeye salmon, suggesting that the UWH was not difficult to find and re-enter after displacement. The proportion of chinook salmon returning in this study was similar to or higher than those reported in previous studies that displaced chinook about 5 km from the UWH (Whitman et al., 1982; Brannon et al., 1986, Quinn et al., 1988). A few of the tagged sockeye in the present study returned over two weeks after release, implying that the sockeye had sufficient time to find and re-enter the UWH before they were too weak.

The 48 sockeye salmon that initially entered the UWH were only 0.005% of the total run of sockeye salmon to the Lake Washington system during the years of this study. We do not infer that this extremely low rate of straying or exploring is representative of spawning sites within this or other lake systems. The absence of odors from conspecific juveniles and trace odors from adults emanating from the UWH might make it less attractive than rivers perennially used by sockeye (Groot et al., 1986), and the small discharge and lack of appropriate habitat for spawning might also deter non-native sockeye from entering. Likewise, the proportions of sockeye salmon straying and exploring in our study may not be representative of those for natural systems.

Entry of sockeye salmon into UWH may differ in some respects from their behavior in natural systems but exploring and straying are characteristic of salmon. On the basis of our results, many of the salmon that enter non-natal hatcheries and that are classified as strays might have left if given the chance. Studies of straying based on recoveries in hatcheries may thus overestimate straying rates, at least in some cases (Quinn et al. 1991). The lack of quantified estimates of proving or exploring behavior makes it difficult to assess whether the high proportion of these patterns found in our study is typical of sockeye or Pacific salmon in general. The distinction between straying and exploring is important to the management of Pacific salmon because CWT-based straying estimates from hatchery populations are commonly used to model interactions between hatchery and wild populations (Grant, 1997), and this subject needs further research.

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Oceanic feeding habits of chinook salmon, *Oncorhynchus tshawytscha*, off northern California

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The chinook salmon, *Oncorhynchus tshawytscha*, is an important commercial and recreational species inhabiting rivers and nearshore coastal waters from San Diego, California, to the Bering Sea and Japan (Miller and Lea, 1972). Many West Coast populations are in a serious decline (Pearcy, 1992). Nehlsen et al. (1991) reported an overall decrease in salmonid numbers in the coastal waters of the Pacific Northwest and suggested that northern California chinook salmon runs may be at high risk of extinction owing to 1) habitat damage and mainstream passage problems; 2) overharvesting; and 3) hybridization, predation, competition, disease, and poor ocean survival conditions. Surprisingly, little research has been done off the northern California coast regarding the diet of salmonids during oceanic migrations.

Studies on the feeding habits of adult chinook salmon have been conducted from San Francisco, California, to southeastern Alaska. Northern anchovy (*Engraulis mordax*), juvenile rockfishes (*Sebastes* spp.), euphausiids, Pacific herring (*Clupea pallasii*), osmerids, and crab megalopae (*Cancer magister*) have been reported as main prey items of chinook salmon ranging from San Francisco to the Washington coast (Heg and Van Hyning, 1951; Merkel, 1957; Petrovich, 1970; Brodeur et al., 1987). Various studies conducted in more northern regions of the Eastern Pacific Ocean have shown Pacific herring and Pacific sandlance (*Ammodytes hexapterus*) as dominant food items (Pritchard and Tester, 1944; Reid, 1961; Prakash, 1962). All of the above studies noted seasonal and or annual differences in the dominant prey items. Overall, it appears that northern anchovy and rockfishes are the most important prey items for chinook salmon in southern coastal regions (i.e. San Francisco Bay area) whereas the importance of Pacific herring and Pacific sandlance increases in more northern regions (Healey, 1991). To adequately describe the trophic resources utilized by a fish population, it is necessary to sample at consistent times throughout the year (Bowen, 1996). Furthermore, in an upwelling zone, such as northern California, the food habits of many fish species may fluctuate considerably between years owing to environmental variability (Brodeur and Pearcy, 1992). For example, diets of pelagic nekton may vary owing to changes in oceanographic conditions, such as onshore and alongshore transport, primary productivity, and prey abundances (Brodeur et al., 1987). In our study, we examined the diet of chinook salmon off northern California. The main objectives were 1) to compare the diet between two consecutive years and 2) to examine seasonal variation in the prey items consumed.

Materials and methods

Stomach samples were collected from fish caught in coastal waters off Humboldt Bay (40°46'N, 124°14'W), Trinidad Bay (41°03'N, 124°09'W), and Crescent City (41°46'N, 124°13'W), California (Fig. 1). From May through September 1994, 196 stomachs were collected from Chinook salmon from the three areas. During 1995, 112 stomachs were collected from the same ports but only in June and September. Approximately 60%, 10%, and 30% of the total stomachs collected were taken from Humboldt Bay, Trinidad Bay, and Crescent City, California, respectively, in both years. Stomach collections were obtained from California Department of Fish and Game (CDF&G) port samplers and directly from sportfishermen. Owing to changing and sporadic season opening dates, as well as to varied placement of port samplers and weather conditions, an unbiased random sampling scheme was not possible. All fish were obtained from the recreational fishery and were greater than or equal to 22 inches (≥56 cm), the CDF&G minimum size limit. Total length measurements were obtained for 54 fish in 1994 and ranged from 59 to 96 cm ($\bar{x}$=74 cm). Although no fish were measured in 1995, they were similar in size to those collected in 1994. This finding suggests that all fish sampled were three to five years of age (Healey, 1991).

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Chinook salmon stomach contents were removed from the digestive tract, fixed in 10% formalin, transferred to 40% isopropyl alcohol, and sorted under a dissecting microscope into major taxonomic groups. When possible, stomach contents were identified to species.

The best measure of dietary importance is one where both the number and weight of a food category are recorded (Hyslop, 1980) . Stomach content data were summarized by four methods: 1) numerical, 2) gravimetric, 3) frequency of occurrence, and 4) index of importance. Each food group was enumerated and weighed from each stomach. Wet weight of prey items was measured to the nearest 0.01 g. By using these data, percentage of total number (*%N*), percentage of total weight (*%W*), and percentage frequency of occurrence (*%F*) were calculated for each food group. "Index of importance" (IOI) was calculated for each food group as follows:

$$IOI_a = \frac{100 \times HI_a}{\sum_{a=1}^{n} HI},$$

where HI_a = $\%F_a + \%W_a$ for food group a; and
n = the number of different food groups (Hannah, 1980; Gray et al., 1997).

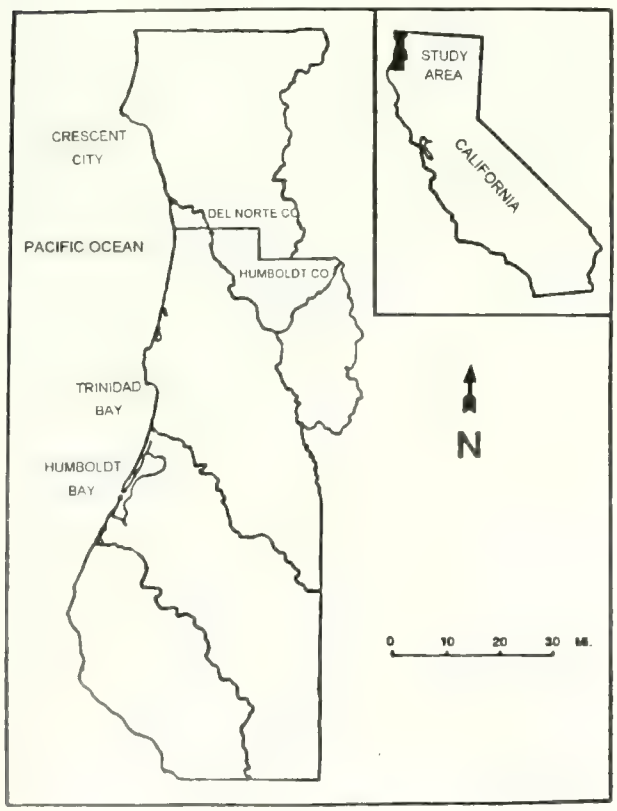

Figure 1
Humboldt Bay, Trinidad Bay, and Crescent City, California.

Because this index calculation is based on *%F* as well as *%W*, the bias towards heavier, infrequently found prey items is reduced.

Results

Values for *%N*, *%F*, *%W*, and *IOI* for prey items encountered in the stomach analyses are listed in Table 1. All stomachs examined (308) contained food items except one from 1994 and two from 1995. Each prey item was present in stomachs sampled from both 1994 and 1995 except for octopi (*Octopus rubescens*) (2), jacksmelt (*Atherinopsis californiensis*) (1), cottids (1), pleuronectids (1), Pacific sandlance (108), and rockfishes (45), which were observed only in 1994 samples and isopods (3) which were present only in 1995 samples. Total values for *%F* did not equal 100% owing to unidentifiable prey items in the diet, especially in 1995 (Table 1).

In 1994, the *IOI* indicated that euphausiids were the predominant food item, accounting for over 27% of the total. Euphausiids not only ranked highest by *%N* and *%F* but also were the leading prey item by *%W*. In addition, notable *IOI* values were observed for crab megalopae, Pacific herring, surf smelt (*Hypomesus pretiosus*), Pacific sandlance, northern anchovy, night smelt (*Spirinchus starksi*), and squid (*Loligo opalescens*). Infrequently encountered prey items included Pacific saury (*Cololabis saira*), rockfishes, amphipods, jacksmelt, octopi, shrimp (mysid), juvenile pleuronectids, and juvenile cottids. In 1995, chinook consumed primarily northern anchovy, which represented over 33% of the total *IOI* but also preyed upon Pacific herring, squid, Pacific saury, surf smelt, night smelt, euphausiids, and crab megalopae. Only rarely were amphipods, isopods, and shrimp found in stomachs. Large interannual variations in *IOI* can be seen for euphausiids, crab megalopae, Pacific sandlance, northern anchovy, squid, and Pacific saury.

Seasonal variation of dominant prey items, for 1994 and 1995, is illustrated in Figure 2, A and B, respectively. In 1994, 88 stomachs were examined from May and June (late spring). *IOI* values for euphausiids (34%), crab megalopae (25%), and Pacific herring (17%) dominated all other prey items. Late summer *IOI* values (based on 108 stomachs acquired in August and September 1994) indicated Pacific sandlance (22%), surf smelt (21%), northern anchovy (17%), and euphausiids (14%) to be major prey items. In 1995, 26 stomachs were examined from fish collected in June and 86 from September. The *IOI* values in our study showed that squid (45%), surf smelt (25%), euphausiids (19%), and Pacific herring (11%) are important prey items in late spring whereas

Table 1

Values for percentages by number (*%N*), frequency (*%F*) and weight (*%W*) for prey items observed in stomachs of chinook salmon, *Oncorhynchus tshawytscha*, collected in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, CA, during the summers of 1994 and 1995.

	1994				1995			
	%N	*%F*	*%W*	*IOI*	*%N*	*%F*	*%W*	*IOI*
Fishes								
Clupea pallasii	0.1	5.6	17.5	12.2	0.5	5.5	17.8	15.7
Engraulis mordax	0.1	3.6	8.7	6.5	8.3	14.6	34.6	33.2
Hypomesus pretiosus	0.1	6.7	12.2	10.0	0.4	2.7	9.6	8.3
Spirinchus starksi	0.2	6.7	4.7	6.0	1.3	2.7	7.0	6.5
Cololabis saira	0.0	1.0	4.3	2.8	1.9	4.6	12.7	11.6
Atherinopsis californiensis	0.0	0.5	0.6	0.6	—	—	—	—
Ammodytes hexapterus	0.4	8.7	9.8	9.8	—	—	—	—
Sebastes spp. (juvenile)[1]	0.2	3.6	1.6	2.7	—	—	—	—
Cottidae	0.0	0.5	0.0	0.3	—	—	—	—
Pleuronectidae	0.0	0.5	0.0	0.3	—	—	—	—
Euphausiid								
Thysanoessa spinifera	71.4	23.1	28.7	27.4	80.8	3.6	5.3	6.0
Crustaceans								
Cancer magister (megalopa)	27.5	19.5	8.6	14.9	2.7	5.5	0.1	3.8
Mysid	0.0	1.0	0.0	0.6	0.1	0.9	0.0	0.6
Amphipoda								
Atylus tridens	0.0	2.1	0.0	1.1	2.6	0.9	0.0	0.6
Isopoda								
Tecticeps convexus / *Synidotea bicuspida* } combined	—	—	—	—	0.2	0.9	0.0	0.6
Cephalopods								
Loligo opalescens	0.1	5.1	3.2	4.4	1.2	6.4	12.9	13.0
Octopus rubescens	0.0	1.0	0.0	0.6	—	—	—	—
Total	100.0	89.2	100.0	100.0	100.0	48.2	100.0	100.0

[1] *Sebastes entomelas, S. mystinus, S. melanops, S. pinniger* (in rank order of abundance)

northern anchovy (49%), Pacific herring (19%), Pacific saury (17%), and night smelt (10%) dominate in late summer.

Discussion

The feeding habits of northern California chinook salmon varied between years and season. This result is consistent with previous studies. Petrovich (1970) found northern anchovy, euphausiids, Pacific herring, osmerids, and rockfishes to be the most important prey items in coastal waters off Humboldt Bay and Trinidad Bay in 1960–1964. As in our study, crab megalopae were especially abundant in one year. In contrast to our results, Petrovich reported rockfishes to be present in 13% of all stomachs from 1960 to 1964, and in terms of frequency of occurrence they ranked third to northern anchovy and euphausiids. We encountered only 45 juvenile rockfishes during our study, all of which came from seven stomachs in the spring of 1994, representing only 2% of all stomachs examined.

Petrovich found relatively few Pacific sandlance and squid, and no Pacific saury in salmon stomachs that he examined. Our study shows that each of these food items contributes significantly to the diet of chinook salmon off Northern California (Fig. 2). Pacific sandlance, although absent in 1995 and only present in small numbers during late spring of 1994, were the major food source (*IOI*=22%) in late summer of 1994. Squid were present in late spring and late summer of both years and greatly outranked (*IOI*=45%) all prey items in late spring 1995. Pacific saury were present in stomachs collected during late summer 1994 (*IOI*=8%) and late summer 1995

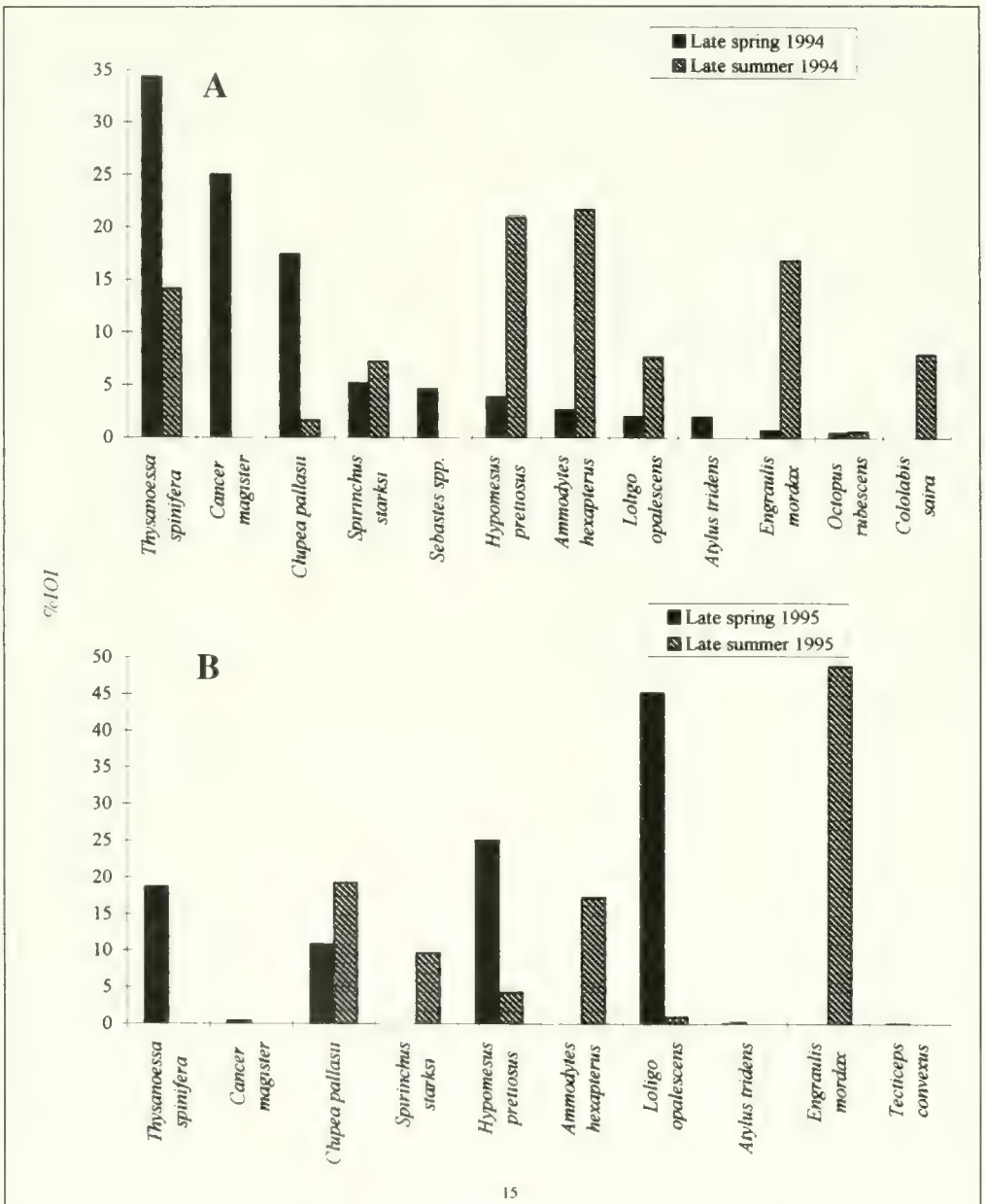

Figure 2

(**A**) 1994 late spring and late summer index of importance (*IOI*) values for predominant prey items consumed by chinook salmon, *Oncorhynchus tshawytscha*, in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, California. (**B**) 1995 late spring and late summer index of importance (*IOI*) values for predominant prey items consumed by chinook salmon, *Oncorhynchus tshawytscha*, in the coastal waters off Humboldt Bay, Trinidad Bay, and Crescent City, California.

(*IOI*=17%). The index of importance indicates that interannual and seasonal variation in the feeding habits of chinook salmon does in fact occur, most likely, in response to variation in the relative abundance of prey along the coast.

Healey (1991) summarized regional trends for coastwide data on chinook feeding habits and recognized that the importance of Pacific herring and Pacific sandlance increased from south to north whereas the importance of rockfishes and northern anchovy decreased. Our data agree with this summary. The diet of chinook salmon off northern California contained characteristic prey items important to chinook found both to the north and south. Although our study

found rockfishes not to be a major prey item of chinook salmon, northern anchovy were in fact commonly taken. In addition, the importance of Pacific herring and Pacific sandlance was substantial. The occurrence of invertebrate prey items (euphausiids, crab megalopae, and squid) during spring months agrees with studies conducted both to the south (Merkel, 1957) and north (Reid, 1961; Prakash, 1962; Brodeur et al., 1987) of the region of our study. Merkel (1957) commonly found euphausiids and squid, April through June, and crab megalopae (presumed to be *Cancer magister*), March through May, in stomachs of fish caught off San Francisco. Similarly, Brodeur et al. (1987), in coastal waters off Oregon and Washington, and Prakash (1962), in British Columbian waters, found euphausiids to be a major prey item during the months of May and June. Prakash also observed an abundance of crab megalopae in chinook diet during June. Squid were a dominant prey item one year in Reid's study off southeastern Alaska during late spring. These results and the great importance of euphausiids, crab megalopae, and squid in our study (Fig. 2) confirm the importance of invertebrate prey, in some years, to chinook salmon.

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The development of the digestive tract and eye in larval walleye pollock, *Theragra chalcogramma**

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First feeding (FF) is a time at which a fish larva must initiate feeding or face starvation that will weaken it and eventually lead to its death. In most oviparous fish with pelagic eggs, organ systems develop that allow larvae to switch from an internal nutrient source (yolk) to an external source (prey) during the time between hatching and FF. Starvation may be a major cause of the high mortalities that occur during the larval period and thus may affect recruitment (Hjort, 1914; O'Connell, 1980; Theilacker, 1986). Indeed, some studies suggest that recruitment is determined in this period (Houde, 1987; Freeberg et al., 1990).

Laboratory experiments show that at FF, the growth rate of walleye pollock, *Theragra chalcogramma*, larvae decreases (Yamashita and Bailey, 1989), or even ceases for a period (Theilacker and Shen, 1993). Furthermore, delaying the introduction of food at FF causes a reduction of the growth rate and size-at-age (Theilacker and Shen, 1993). These studies indicate that FF walleye pollock lack energy reserves, and thus the availability of nutritious prey at this time is critical. Theilacker and Porter (1995) found that the largest proportion of starving walleye pollock larvae in Shelikof Strait, Gulf of Alaska, are in the size class that includes FF larvae. Thus, the FF period appears to be the time when walleye pollock larvae are most vulnerable to starvation. Studies involving larvae of other marine fish have found similar results (Atlantic mackerel, *Scomber scombrus*, Ware and Lambert, 1985; jack mackerel, *Trachurus symmetricus*, Theilacker, 1986).

Larval walleye pollock survival is dependent upon timely development of organs required for feeding. Of the many developmental changes occurring during the early larval period, two of the most important for walleye pollock may be vision and the digestive tract. Eyesight is probably the most important sense walleye pollock larvae use in finding prey because they are visual predators (Paul, 1983) and do not use chemosensory cues (Davis and Olla, 1995). Digestive tract development is important for efficient assimilation of nutrients needed for growth. In this study, histological sections were used to describe the development of the mouth, digestive tract, and eyes in laboratory-reared walleye pollock, from hatching to 31 days after hatching (DAH), to examine how organs necessary for feeding develop. This is essential to an understanding of why walleye pollock larvae are most vulnerable to starvation during the first week of feeding.

Materials and methods

In 1991 and 1992, adult walleye pollock were collected from Shelikof Strait, Gulf of Alaska, and spawned aboard ship. Fertilized eggs were maintained aboard ship at 3°C for a few days, then transported to the laboratory. In 1991, walleye pollock larvae were reared at Friday Harbor Laboratories, University of Washington, San Juan Island, Washington, and in 1992, at the Alaska Fisheries Science Center, Seattle, Washington. Between 500 and 1000 larvae were reared in a black, circular, 120-L fiberglass tank (62 cm diameter, 43 cm deep) filled with 90 L filtered seawater (salinity=28.0 ±0.5 ppt) and maintained at 6° ±0.5°C, the typical seawater temperature in Shelikof Strait when walleye pollock larvae initiate feeding (Kendall et al., 1987). Larval rearing procedures followed Porter and Theilacker 1996.[1]

Fluorescent fixtures were used with a 16-hour light cycle; the amount of light at the surface of the water in the rearing tank was 17 μ mol photon/m^2/s. Prey consisted of the rotifer *Brachionus plicatilis*, raised on an algal diet of *Isochrysis galbana* and *Pavlova lutheri* high in unsaturated fatty acids (Nichols et al., 1989), as well as of *Acartia* sp. copepod nauplii and copepodites collected from a local lagoon. At 3 DAH, four to five days before FF, rotifers were added at 10/mL and *Acartia* were added at 3/mL to the rearing tank and maintained at this level throughout the rearing

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[1] Porter, S. M., and G. H. Theilacker. 1996. Larval walleye pollock, *Theragra chalcogramma*, rearing techniques used at the Alaska Fisheries Science Center, Seattle Washington. AFSC processed report 96-06, 26 p. U.S. Dep. Commerce, NOAA, NMFS, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA., 98115.

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period. Eight to 10 larvae were sampled every day or every other day after hatching to 23 DAH in 1991 and to 31 DAH in 1992. Larvae were placed into either Bouin's fixative which was replaced with 70% ethanol 24 to 48 h later, or Z-fix[2] (a solution of 10% formalin with zinc and buffers added). Larvae were dehydrated in a graded series of butyl alcohols, embedded in paraffin wax, sectioned sagittally into 6-µm serial sections, and stained with hematoxylin and eosin (H and E). Standard lengths (SL, tip of upper jaw to end of notocord) of preserved larvae were measured to the nearest 0.08 mm and adjusted to live SL (Theilacker and Porter, 1995). To describe development of the mouth, digestive tract, and eyes, histological sections of 5–10 larvae were examined from each sampling day.

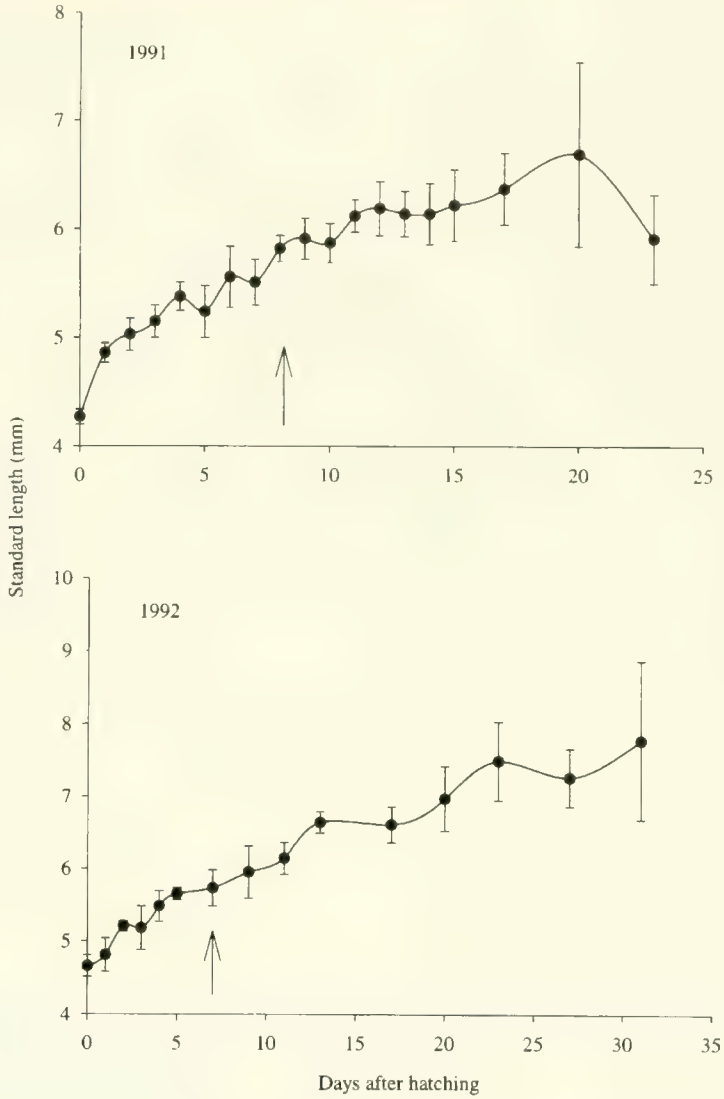

Figure 1

Growth of walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory from hatching to 23 days after hatching in 1991, and to 31 days after hatching in 1992. Mean standard length (preserved length adjusted to live length, see text) and standard deviation are shown; 5 to 10 larvae were measured at each age. The small size for 1991 at 23 days after hatching may be due to sampling slow growing larvae in poor condition (see text). Arrow indicates day of first feeding.

Results

Larval growth

In 1991, the mean SL at hatching was 4.27 ±0.07mm, whereas in 1992 hatching size averaged 4.66 ±0.15mm (Fig. 1). The decrease in average size of larvae sampled on day 23 in 1991 (Fig. 1) was probably due to the sampling of slow growing larvae in poor condition. A bowl was used to sample larvae from the tank, and we suspect that for this sample only slow growing larvae were captured. The overall mean growth rate from hatching to 20 DAH was 0.12 mm/d in both 1991 and 1992. In 1992, experiments continued until 31 DAH and average growth from hatching was 0.10 mm/d. The onset of FF occurred over a period of three days; day of first feeding was defined as the time when 50% of the larvae began feeding. In 1991, day of first feeding occurred at 8 DAH, and the mean SL was 5.82 ±0.12 mm. In 1992, larvae began feeding at 7 DAH, and the mean SL was 5.73 ±0.25 mm (Fig. 1).

Mouth and digestive tract development

At hatching a membrane covered the mouth, and jaw cartilage had not yet formed. At 2 DAH the membrane began to degenerate leaving an orifice that was 22 to 55 µm wide. Mouth and jaw cartilage also began forming at this time, and the cartilage in the roof of the mouth, the trabeculum cranii, became most distinct. All jaw cartilage elements were present and almost completely formed at 5 DAH (approximately 2 days before FF); the mouth was considered functional 5 to 6 DAH (Table 1).

At hatching the gut was a straight tube with a narrow lumen. The foregut could be distinguished

[2] Anatech, Ltd., Battle Creek, MI.

Table 1

Mean standard length (tip of upper jaw to end of notocord) and age at the development of various elements of the mouth, digestive tract, and eye for walleye pollock, *Theragra chalcogramma*, reared at 6°C in the laboratory in 1991 and 1992. '+', vacuoles were not observed at 23 DAH in 1991, the last sampling day. Preserved standard length adjusted to live standard length (Theilacker and Porter, 1995). SD = standard deviation. *n* = number of larvae measured. Age = days after hatching.

	Mean standard length mm (SD)				
	1991	*n*	1992	*n*	Age (year)
Mouth and digestive tract					
Foregut, midgut, and hindgut separated by valves	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Jaw developed and mouth functional	5.56 (0.28)	5	5.65 (0.08)	5	5 (1992) 6 (1991)
Folding of midgut epithelium	6.19 (0.25)	5	6.14 (0.22)	10	11 (1992) 12 (1991)
Midgut coiling, eosinic vesicles in the hindgut	6.14 (0.28)	5	6.64 (0.15)	8	13 (1992) 14 (1991)
Lipid vacuoles in midgut	+		7.49 (0.54)	10	23 (1992)
Eye					
Ocular motor muscles apparent	5.15 (0.15)	5	5.18 (0.30)	5	3 (1991,92)
Eye fully pigmented	5.38 (0.13)	5	5.48 (0.21)	5	4 (1991,92)
Lens retractor muscle developed	6.22 (0.33)	5	no samples taken		15 (1991)

by its cuboidal epithelium, but no distinction could be made between the midgut and hindgut which were lined with similar columnar epithelium. At 1 DAH, the gut lumen widened and began to separate into a long midgut and short hindgut that were demarcated by a constriction at the future site of the ileocaecal valve. At 3 DAH, the pyloric valve separated the foregut and midgut, and the ileocaecal valve separated the midgut and hindgut (Table 1; Fig. 2). At 11 to 12 DAH (4 days after FF) the gut began to develop large folds, and began to coil 13 to 14 DAH (6 days after FF) (Table 1). Also, at 13 to 14 DAH, eosinic vesicles (also referred to as eosinophilic granules or inclusions), ranging in size from 1 to 3 μm, began appearing in the apical cytoplasm of the hindgut epithelial cells (Table 1). Vacuoles in midgut epithelial cells were first observed at 23 DAH in 1992 larvae (Table 1). The vacuoles were not distinct and observed only in one larva out of ten. Walleye pollock larvae showed no other changes in gut structure (i.e. no stomach, or pyloric caeca) up to 31 DAH.

Eye development

At hatching, a lens was present, and small scattered patches of pigment were located throughout the retina (Fig. 3). The pigment patches increased in size and joined to form the pigment layer; by 4 DAH the eye was fully pigmented (Table 1). Ocular motor muscles were not developed at hatching, but at 3 DAH these muscles became apparent (Table 1). At 9 DAH, the lens retractor muscle was identified as a thin structure that connected the lens to the retina. From 9 to 15 DAH the muscle increased in width as it grew. The size and shape of this muscle changed very little beyond 15 DAH; therefore it was considered functional beginning at this time (Fig. 4, Table 1).

Discussion

Larval growth

Growth of walleye pollock larvae in this study was similar between years (0.12 mm/d from hatching to 20 DAH for both 1991 and 1992) and to rates found by others for walleye pollock larvae reared at 6°C in the laboratory; 0.14 mm/d from hatching to 19 DAH (Theilacker and Shen, 1993), 0.11 mm/d from hatching to 21 DAH (Yamashita and Bailey, 1989) and 0.065 mm/d from hatching to 15 DAH (Nishimura and Yamada, 1984). Growth was slightly lower than the 0.14 to 0.23 mm/d calculated for field-collected walleye pollock larvae (Bailey et al., 1996).

Mouth and digestive tract

From observations on live larvae, Bailey and Stehr (1986) found that walleye pollock have no mouth at hatching; the mouth begins to develop 2 days later

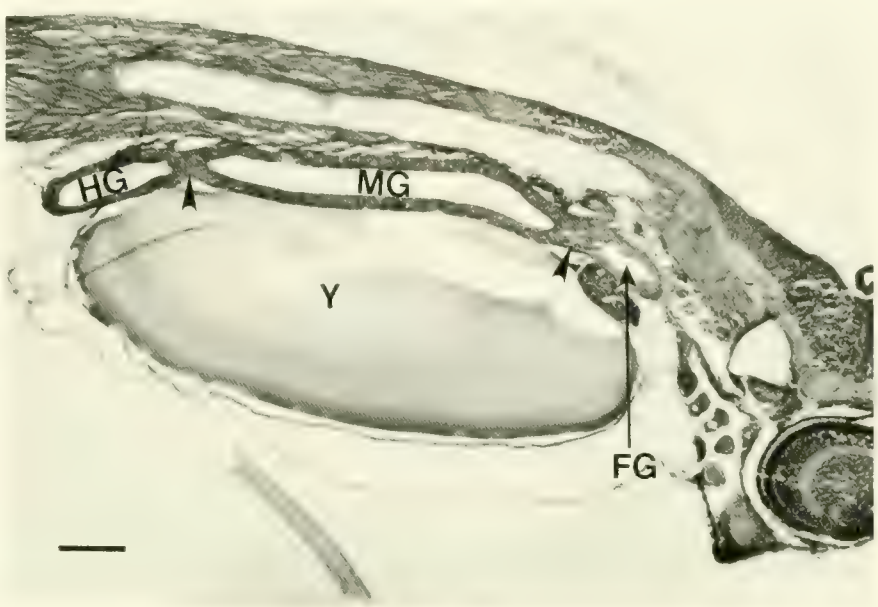

Figure 2

Walleye pollock, *Theragra chalcogramma*, larva 3 days after hatching. The foregut (FG) and midgut (MG), and midgut and hindgut (HG) are separated by the pyloric and ileocaecal valves respectively (arrowheads). (Bouin's fixative, H and E; standard length=5.24 mm; scale bar=100 μm). Y = yolk.

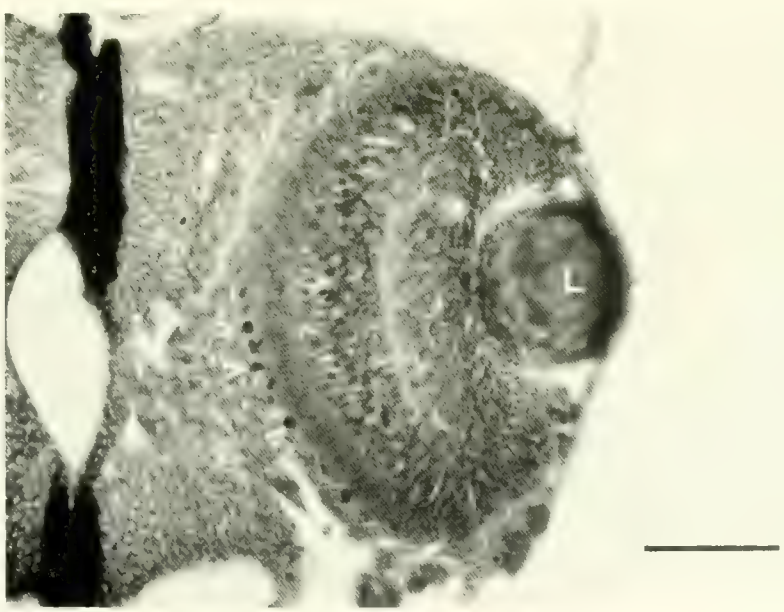

Figure 3

Walleye pollock, *Theragra chalcogramma*, eye at hatching. The eye is not fully pigmented. Arrowheads identify patches of pigment. (Bouin's fixative, H and E; standard length=4.34 mm; scale bar=50 μm). L = lens.

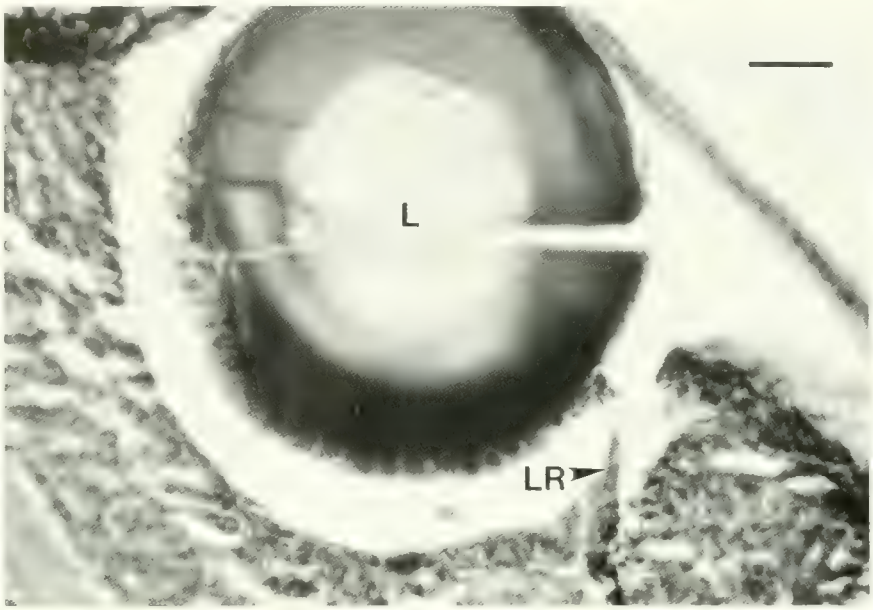

Figure 4

The lens retractor muscle (LR) in the eye of a 15-day posthatching walleye pollock, *Theragra chalcogramma*, larva. (Bouin's fixative, H and E; standard length=6.65 mm; scale bar=20 μm). L = lens.

and is functional by 4 to 5 DAH. Histological analysis in this study showed that mouth and jaw development proceeded at a similar rate; the jaw was fully formed and the mouth was functional 5 to 6 DAH. As in Atlantic cod, *Gadus morhua*, larvae (Kjørsvik et al., 1991), the first feature of the walleye pollock mouth to form was the trabeculum cranii ("roof of the mouth").

At hatching, walleye pollock larvae had a straight-tube gut. This simple gut arrangement has been noted for larvae of other species of fish as well (northern anchovy, *Engraulis mordax*, O'Connell, 1981; Atlantic cod, *G. morhua*, Kjørsvik et al., 1991; turbot, *Scophthalmus maximus*, Segner et al., 1994). At 3 DAH, three distinct portions of the gut could be identified: the foregut, midgut, and hindgut. This gut arrangement is typical of larval fish (Govoni et al., 1986) and walleye pollock larvae showed no major changes in gut structure (i.e. no stomach, or pyloric caeca) up to 31 DAH. For larval fish, major changes in gut structure happen rapidly at metamorphosis rather than gradually during the larval period (Govoni et al., 1986). However, at 11 to 12 DAH (4 days after FF) the larval walleye pollock midgut epithelium began to develop large folds, and the gut began to coil 13 to 14 DAH (6 days after FF). For walleye pollock larvae reared at 6°C, Oozeki and Bailey (1995) noted that gut coiling began on 16 DAH and was complete by day 23. Midgut coiling increases the length of the gut, and the residence time of prey in it (Yamashita and Bailey, 1989). At one week after FF, both epithelial folds and gut coiling enable walleye pollock larvae to assimilate nutrients more efficiently through increased absorptive surface area and longer residence times.

Histological evidence suggests the larval walleye pollock gut functions in the same manner as in other fish larvae. The midgut of fish larvae digests and absorbs lipids (Govoni et al., 1986) and this appears to be the function of the larval walleye pollock midgut as well. For larval whitefish, *Coregonus fera*, lipid vacuoles appear as circular "voids" in the apical portion of the midgut epithelial cells one day after feeding (Loewe and Eckmann, 1988). In other species of fish, similar vacuoles are also reported to contain lipid (goldfish, *Carassius auratus*, Iwai, 1968; turbot, *S. maximus*, Segner et al., 1994). In our study, vacuoles (circular voids) were observed in midgut epithelial cells of one walleye pollock larva at 23 DAH. This is later in development than they have been observed in other fish larvae but lipase is present in walleye pollock larvae at hatching; therefore lipid digestion could occur at FF. Lipase activity increases with age (Oozeki and Bailey, 1995) so that as larvae grow, more lipid can be digested and this could produce larger, more visible (by H and E stain-

ing) vacuoles with age. There was probably lipid in the midgut cells earlier than 23 DAH but in such small amounts so that it could not be identified without special staining. The larval walleye pollock hindgut appears to function in protein digestion like the hindgut of other species of fish larvae (Govoni et al., 1986). Watanabe (1984) demonstrated that protein is pinocytotically moved into hindgut epithelial cells for intracellular digestion. Iwai and Tanaka (1968) stated that the intracellular protein appears as eosinophilic granules (also referred to as eosinophilic vesicles or inclusions) within the apical portion of the hindgut cells. At 13 to 14 DAH (5 to 7 days after FF), eosinic vesicles appear in the apical cytoplasm of the hindgut epithelial cells of walleye pollock larvae. For Atlantic cod, *G. morhua*, larvae (Kjørsvik et al., 1991), a close relative of walleye pollock, inclusions were not observed until 2 to 5 days after FF. In other studies eosinophilic inclusions have been observed soon after FF (northern anchovy, *E. mordax*, O'Connell, 1981; whitefish, *C. fera*, Loewe and Eckmann, 1988; turbot, *S. maximus*, Segner et al., 1994). Trypsin is present in walleye pollock larvae at hatching, its activity increases with age, and it is not supplemented by prey in the gut (Oozeki and Bailey, 1995). Eosinophilic vesicles appeared at the time the gut began to coil, and both coiling and increased trypsin would allow increased digestion of prey making more protein available to the hindgut, possibly explaining why vesicles were not apparent until some time after FF. The appearance of lipid vacuoles and eosinophilic vesicles after the first week of feeding provides evidence for improved digestive capability.

Eye

Sight is probably the most important sense walleye pollock larvae use for feeding. Walleye pollock rely on vision to search for prey (Paul, 1983) and do not respond to chemosensory cues (Davis and Olla, 1995). Laboratory experiments show that a group of walleye pollock larvae, age 21 DAH, remains aggregated when rotifers are introduced into the group, but when only the scent of rotifers is introduced, the group disperses (Davis and Olla, 1995). Because they are visual predators and because light below 0.006 μ mol photon/m^2/s limits their ability to capture prey (Paul, 1983), walleye pollock larvae probably have a pure-cone retina like many other species of fish larvae. Blaxter and Staines (1970) examined the retina of 12 species of fish larvae including haddock, *Melanogrammus aeglefinus* (which belongs to the same family as walleye pollock, Gadidae), they showed that haddock and seven other species have a pure cone retina. Olla and Davis (1990) stated that the retina of walleye pollock larvae most likely does not contain rods. It is unknown when rods begin to appear in walleye pollock, but for herring, *Clupea harengus* (Blaxter and Jones, 1967), plaice, *Pleuronectes platessa* (Blaxter, 1968), and sole, *Solea solea* (Sandy and Blaxter, 1980), rods begin to appear at metamorphosis.

The lack of eye pigmentation at hatching has been found for many teleosts (Blaxter, 1986), including walleye pollock (Bailey and Stehr, 1986; our study), and eyes are probably nonfunctional at this time (Blaxter, 1986). Ocular motor muscles developed just as walleye pollock eyes became fully pigmented (3 DAH). The development of eye pigmentation and ocular motor muscles should provide a FF larva with sight and the ability to move its eyes. The lens retractor muscle did not develop until after FF; it was considered functional beginning at 15 DAH. The lens retractor muscle develops after FF in other species of fish as well (northern anchovy, *E. mordax*, O'Connell, 1981; white seabass, *Atractoscion nobilis*, Margulies, 1989). This muscle allows a larva to focus on objects at different distances, thereby increasing the field of vison (Munz, 1971). Because this muscle was not functional until 15 DAH, for about a week after FF a larval walleye pollock's field of view is restricted because it is unable to change the focus of its eyes. Thereafter, visual acuity improves, allowing walleye pollock larvae to detect both prey and predators more easily.

In Shelikof Strait, Gulf of Alaska, the proportion of starving walleye pollock larvae decreases dramatically after the first week of feeding (Theilacker and Porter, 1995; Theilacker et al., 1996) and the physiological condition of walleye pollock larvae improves as they grow; that is, fewer larvae are found in poor condition (Theilacker et al., 1996). Improvements to vision (the lens retractor muscle) and a combination of morphological changes to the gut (folding and coiling) as well as an increase in digestive enzymes (Oozeki and Bailey, 1995) contribute to walleye pollock larvae becoming less vulnerable to starvation after the first week of feeding. Additional contributing factors may include developmental changes occurring to other organ systems (e.g. development of trunk musculature and lateral line system as has been shown for other species of fish larvae; Blaxter, 1986; O'Connell, 1981), and larvae becoming better predators as they grow. For northern anchovy, *E. mordax*, larvae, feeding success rapidly improves during the first week of feeding (Hunter, 1972). At hatching walleye pollock larvae lack functional eyes and mouth, and have a straight-tube gut; the development of these between hatching and FF allows larvae to begin feeding, and their continued development after FF improves the larvae's chance of survival.

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Evaluation of small T-anchor and dart tags for use in marking hatchery-reared juvenile red drum, *Sciaenops ocellatus*

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Red drum, *Sciaenops ocellatus*, is an estuary-dependent marine species found in coastal and nearshore waters in the western Atlantic Ocean from Maine to Florida and in the Gulf of Mexico from Florida to Vera Cruz, Mexico (Yokel, 1966, 1980). Red drum are highly sought after as food and gamefish. Annual commercial landings in Florida averaged nearly 1.0 million pounds from the early 1960s until 1986, when the sale of red drum was prohibited. Recreational fishing effort directed toward red drum in Florida has more than doubled since 1989 on both the Atlantic and Gulf coasts (Murphy[1]). Increased fishing pressure on red drum stocks has led to the implementation of various management strategies, such as closing the commercial fishery and reducing the recreational catch by means of bag limits, size limits, and closed seasons. In the 1970s, methods were developed for culturing red drum in controlled hatchery environments, providing a pathway for the use of stock enhancement for managing the fishery (Arnold et al., 1977; Roberts et al., 1978a, 1978b). Red drum stock enhancement has been conducted extensively in Texas and, to a lesser degree, in Florida and South Carolina (Matlock et al., 1986; Willis et al., 1995; Smith et al.[2]).

Monitoring stocked fish populations in the wild is critical in determining the impact of stocked fish on the fishery and the natural population. Red drum are stocked at various sizes: (phase-1 (25–50 mm SL); phase-2 (50–100 mm SL); and phase-3 (100–200 mm)). Stocking larger size red drum (phase-2 or -3), facilitates the use of tagging as a method of tracking these fish in the wild. Tagged fish can provide valuable data on stock identity, fishing pressure, movements, abundance, age and growth, mortality, and stocking-program success (Ricker, 1956; Hilborn et al., 1990; McFarlane et al., 1990). However, the usefulness of these data depends on knowledge of tag-retention rates and of the effects of tagging on fish growth and survival.

A variety of tag types have been tested on red drum of various sizes. Several studies have evaluated the use of coded wire tags in juvenile red drum (phase-2, 50–100 mm SL, Bumguardner et al., 1990, 1992; Szedlmayer and Howe, 1995). Because coded wire tags are not externally visible, recreational and commercial fishermen are not likely to see them and therefore are not likely to submit capture data to authorities; externally visible tags are better suited for obtaining capture information from recreational and commercial fishermen.

Externally visible tags are typically restricted to use in red drum larger than 100 mm (phase-3 fish). Retention of externally visible tags in phase-3 red drum (100–200 mm SL) has not been rigorously tested, and little is known of the effects of these tags on survival or growth in this size of red drum. Some studies have tested the effects of various external tags on large red drum (>300 mm SL; Elam, 1971; Weaver, 1976; Hein and Shepard, 1980a; Gutherz et al., 1990). Matlock et al. (1984) reported using Monel jaw tags and Willis et al. (1995) reported using internal-anchor tags in fingerling red drum (100–200 mm SL), but neither report addressed tag-retention rates or effects of tags on growth or survival.

The Florida Department of Environmental Protection's Stock Enhancement and Research Facility (SERF) has the capability of rearing phase-1, -2, and -3 red drum for release. Data from this study were used to evaluate the efficacy of two types of external tags in hatchery-reared phase-3 juvenile red drum, and to provide tag-retention and survival estimates, which are necessary for correctly interpreting capture information.

Materials and methods

Retention of T-anchor and dart tags in hatchery-reared red drum (102–173 mm SL) was evaluated over a 423-day period. Mortality associ-

[1] Murphy, M. D. 1994. A stock assessment for red drum, *Sciaenops ocellatus*, in Florida. Florida Marine Research Institute. Report to the Fla. Mar. Fish. Comm., Tallahassee, FL, 28 p.

[2] Smith T. I. J., M. R. Denson, D. B. White, and W. E. Jenkins. 1993. Evaluation of a preliminary red drum stock enhancement program in South Carolina. SC Wildl. Mar. Res. Dep., Mar. Resour. Res. Inst. Annu. Performance Rep. Charleston, SC, 21 p.

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Fish. Bull. 97:730–735 (1999).

ated with tagging was monitored for the first 111 days of the experiment.

T-anchor tags (IEX tags[3], Fig. 1) had an 18-mm "T" with molded polyethylene on both sides for support. Attached to the "T" portion of the tag was a 42-mm streamer, the distal two-thirds of which was encased in polyethylene. T-anchors were inserted through a 1-mm-diameter hole made with a pointed, stainless-steel rod. Tags were inserted on the left ventral side of the fish near the distal end of the pelvic fin. Once inserted, the tag streamer was pulled so that the T-anchor rested along the body cavity wall, with the streamer protruding.

Dart tags (PDX tags[2], Fig. 1) had a 9-mm, semi-rigid plastic barb attached to a 45-mm plastic streamer that was encased in polyethylene. Dart tags were inserted into the pterygiophores of the spinous dorsal fin by using a stainless-steel canula.

We dipped all tags and applicators in Betadyne before tagging each fish to minimize the possibility of infection. The streamer of each tag was imprinted with a unique tag number so that we could identify individual specimens.

All red drum used in this experiment were spawned and maintained in ponds at the Florida Department of Environmental Protection's Stock Enhancement Research Facility (SERF) in Port Manatee, Florida. The holding ponds were drained at 290 days after spawning and fish were dip-netted to a small holding tank, where they were anesthetized (Tricaine menthanesulphonate, MS222, 100 ppm). Fish were measured (SL mm) and randomly assigned to one of three treatment groups: dart tagged, T-anchor tagged, and controls (handled but not tagged). Each treatment group contained 100 fish (mean SL=140 mm, mean weight=40 g), divided equally between two 1.5-m-diameter net pens with a volume of 2.12 m^3. Net pens were constructed of 6.25-mm knotless nylon mesh and were submerged within a closed aquarium system (>79,000 liters) with supporting aeration, bio-filter, and rapid sand filter. Salinity (‰), dissolved oxygen (mg/L), and temperature (°C) were monitored daily. Ammonia concentration (NH_3^+, mg/L) was monitored periodically. Fish were fed a combination of cut squid and commercially prepared pelletized fish food at a rate of 2–5% of body weight per day.

Net pens were checked daily for fish mortalities and shed tags. Standard length (SL mm), date, tag type, tag number, and pen number were recorded for all fish mortalities. At 66, 111, and 423 days after tagging (DAT), fish from all net pens were measured (SL mm), tag numbers checked, and tag wounds observed for degree of healing (wound open or closed). Control fish were removed from the study at 111 DAT. We continued to monitor tagged fish from 111 to 423 DAT so that we could evaluate long-term tag retention. All fish were treated for *Amyloodinium* sp. and parasitic copepods at 21 DAT.

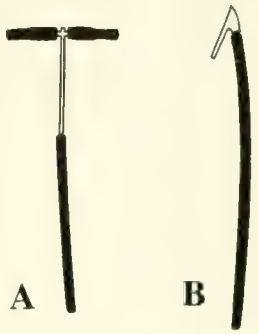

Figure 1
External tags used to mark hatchery-reared red drum: (**A**) T-anchor (IEX tags) and (**B**) dart (PDX tags). Both tags are manufactured by Hallprint Ltd., Holden Hill, Australia. Shown at 75% of actual size.

Standard length measurements of red drum were compared between net pens at 0, 66, and 111 DAT by using a nonparametric Kruskal-Wallis one-way ANOVA on ranks test (α=0.05). Instantaneous survival rates of red drum were compared between treatments by using a two-way (% of fish alive) repeated measures ANOVA (α=0.05) on arcsine-transformed data. Net pen was used as the subject, with tag type as a group factor and days as a level factor (Fox et al., 1995).

Results and discussion

Tag-retention rates in red drum in this study were similar for both T-anchor and dart-tagged fish (Table 1). Average retention rates for T-anchor and dart tags were, respectively, 98% and 99% at 66 DAT; 97% and 95% at 111 DAT; 91% and 89% at 423 DAT. No tags were shed until 41 DAT, and nearly all shedding stopped by 150 DAT (Fig. 2). Both tag types were retained in some red drum as large as 485 mm SL. Wallin et al. (1997) also reported high short-term (30 days) retention rates (100%) of T-anchor tags in ju-

[3] Hallprint Ltd., 27 Jacobsen Crescent, Holden Hill, South Australia 5088, Australia.

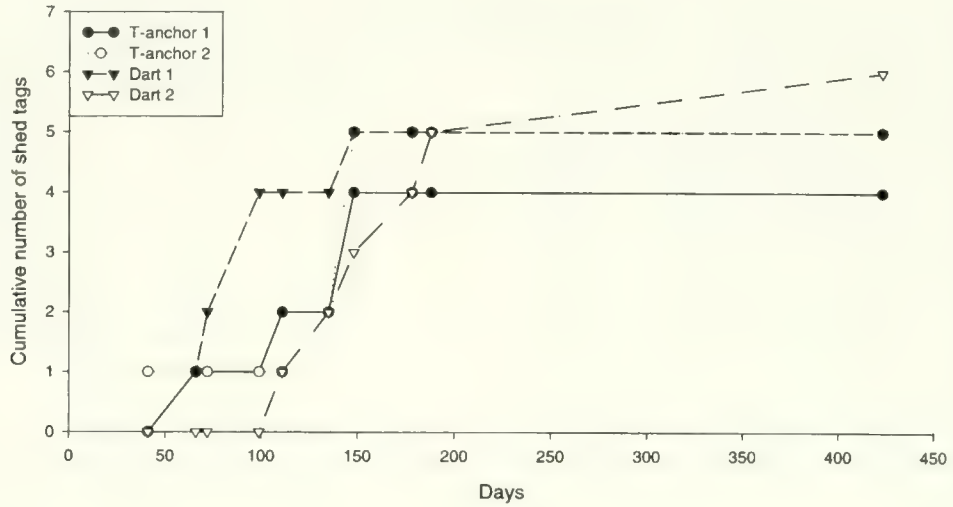

Figure 2

Cumulative number of tags shed by hatchery-reared red drum over a 423-day period. Each tag type was tested in two separate mesh-net pens, each holding 50 fish at start of test.

venile *Centropomus undecimalis*. Collins et al. (1994) found that T-anchor tags had higher long-term retention rates than did dart tags in juvenile *Acipenser brevirostrum* (T-anchor: 92% at 306 DAT; Dart: 50% at 154 DAT). The low retention rates of dart tags in their study may be explained by the fact that the posterior position of the dorsal fin in these fish subjected the tags to the constant motion of the caudal fin and thus enlarged the wound around the tag insertion point (Collins et al., 1994).

Compared with other external tags, T-anchor and dart tags appear to have superior retention rates in small red drum (<380 mm SL). Floy dorsal, Monel metal operculum, Monel metal jaw, Petersen operculum, Petersen dorsal, streamer dorsal, and Carlin dangler tags all yielded lower retention rates (<50% after 154 DAT, Hein and Shepard, 1980a) than did the T-anchor and dart tags tested in this study.

At 66 and 111 DAT, none of the T-anchor tag wounds had healed. Other studies have also shown that tag rotation and movement irritated the incision site, inhibited healing, and left an opening into the body cavity (Smith et al., 1990; Collins et al., 1994). Wallin et al. (1997) suggested that long-term retention of T-anchor tags may be reduced because of the open tag wounds; this was not observed in the 423 days of our study. The anchor portion of some of the T-anchor tags protruded through a hole in the abdominal wall that was separate from the tag insertion point. This may have been an early stage of tag shedding, although it was never verified that the protruding tags were actually shed. Similar results have also been reported in studies with disk-type internal-anchor tags (Vogelbein and Overstreet, 1987; Mattson et al., 1990).

All dart-tag wounds appeared to be healed by 66 DAT. Increases in fish body size during the course of the study caused the streamer portion of some dart tags to become engulfed by the body-wall tissue. This made the tags difficult to detect and impossible to read without dissection. A longer tag streamer could minimize this effect, but it could increase stress on smaller fish during tagging. Simmons and Breuer (1982) also reported tissue growth over tags, which reduced the ability to identify tagged red drum.

Tagging did not appear to adversely affect red drum survival. There was no significant difference in instantaneous survival estimates between treatments (F=2.2, P=0.26). Mean percent survival of control, T-anchor, and dart-tagged fish was, respectively, 79%, 68%, and 79% at 66 DAT and was 67%, 65%, and 77% at 111 DAT (Table 1). Nearly all mortality occurred during the first 40 days of the experiment; 67% of all T-anchor and 83% of all dart-tag mortalities occurred during this time period (Fig. 3). These results are consistent with those of other studies in which these tag types were used (Collins et al., 1994; Szedlmayer and Howe, 1995; Wallin et al., 1997).

Initial lengths of red drum were not significantly different between treatments (H=3.1, P=0.68, df=5, Table 1). Red drum lengths at 66 and 111 DAT were also not significantly different between treatments (66 DAT: H=3.9, P=0.56, df=5; 111 DAT: H=6.4, P=0.27, df=5), suggesting that tagging did not ad-

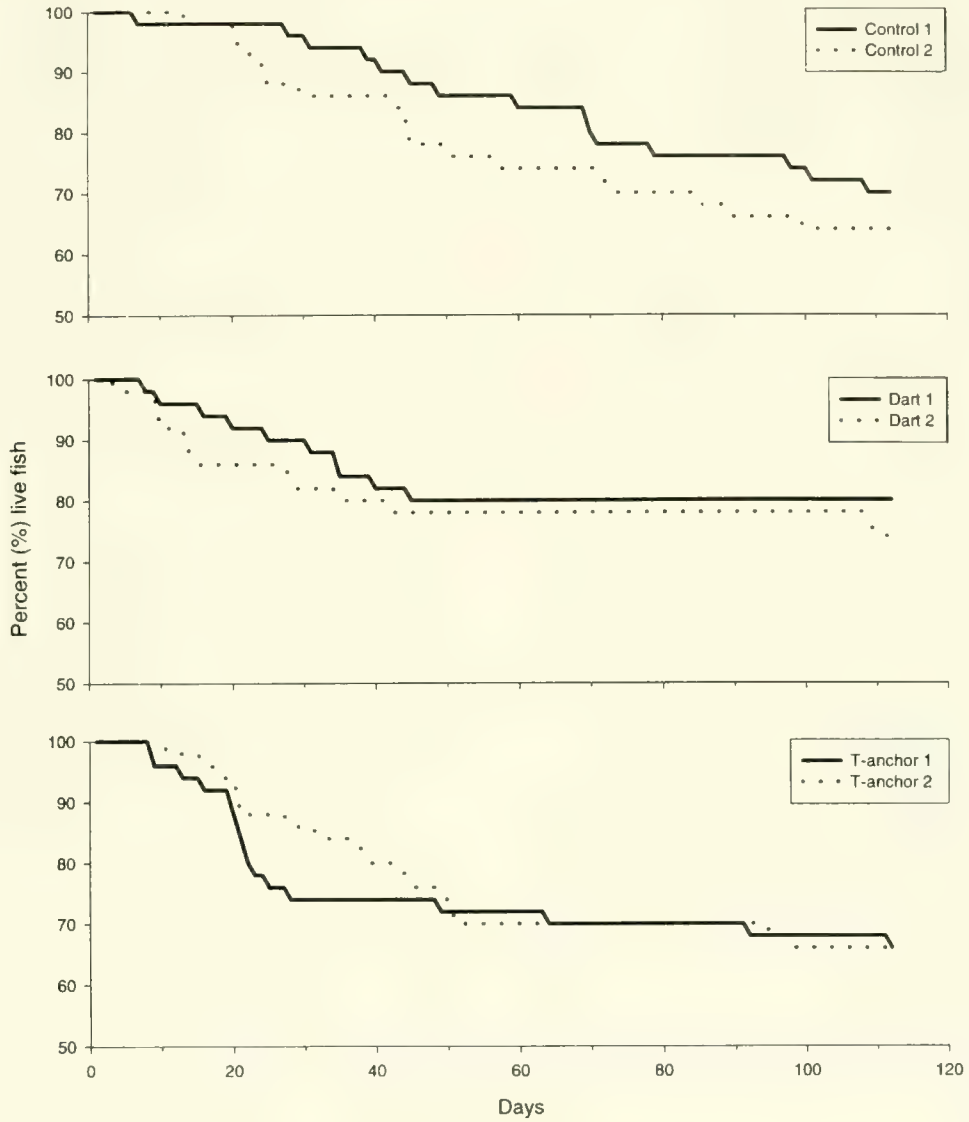

Figure 3
Survival of red drum in each treatment group during the first 112 days of the study.

versely affect fish growth. It is important that a tagging method not affect growth (Ricker, 1956; Wydoski and Emery, 1983), especially when tagging is being used to verify aging methods (e.g. oxytetracycline injection) or to estimate survival rates in the wild (Green et al., 1985; McFarlane et al., 1990). Growth-rate estimates of red drum in our study (0.41–0.50 mm/day) were lower than those for this size of red drum reported in other studies (Colura and Hysmith, 1975; Hein and Shepard, 1980b), possibly because of the high stocking densities in the net pens.

In summary, dart and T-anchor tags are well suited for marking juvenile phase-3 red drum (102–173 mm SL) and are usually retained until the fish are large enough to enter the fishery (Florida minimum size limit for red drum is 368 mm SL). Both tag types were easy to apply and did not affect red drum growth or survival. Although tag retention, survival, and growth rates did not differ between tag types, our results did reveal some potential problems associated with the long-term use of T-anchor tags. The wound around the insertion point of the T-anchor tags did not heal during the 423 days of our experiment, and late in the study, some tags showed signs of expulsion (anchor protrusion through abdominal wall). Both tag types could be used to track releases of

Table 1

Cumulative percent red drum survival (66 and 111 days after tagging (DAT) and tag retention (66, 111, and 423 DAT) for all treatments. Each treatment was replicated in two separate mesh-net pens, each of which held 50 hatchery-reared red drum. Mean standard lengths (mm) and associated standard errors (in parentheses) are also listed for 0, 66, and 111 DAT.

		% Survival DAT		% Tag retention DAT			Mean standard length, mm (standard error) DAT		
Treatment/Pen#		66	111	66	111	423	0	66	111
Control	1	84	50	—	—	—	140 (2.21)	166 (2.87)	195 (3.65)
	2	74	64	—	—	—	136 (2.12)	160 (3.13)	191 (3.23)
T-anchor	3	70	66	98	96	92	138 (1.57)	167 (2.60)	191 (3.05)
	6	66	64	98	98	90	141 (1.88)	163 (2.68)	188 (3.91)
Dart	4	80	80	98	92	90	140 (1.84)	165 (2.70)	184 (3.71)
	5	78	74	100	98	88	138 (1.60)	161 (2.22)	184 (2.28)

hatchery-reared phase-3 red drum and thus allow scientists to monitor and accurately determine the effects such releases have on naturally occurring stocks.

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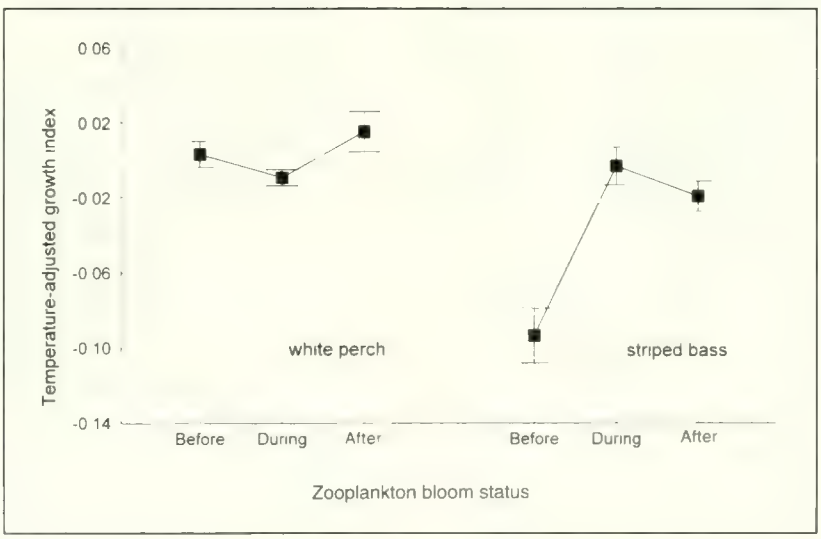
Erratum

Erratum: Fishery Bulletin 97(1):80–91
Limburg, Karin E., Michael L. Pace, and Kristin K. Arend
Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River

Correction: Karin Limburg has pointed out that the graphs in Figure 2 (p. 85) were mislabeled. Please find below the correct graphs for white perch and striped bass.



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Larval development of *Symphurus williamsi* (Cynoglossidae: Pleuronectiformes) from the Gulf of California

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Abstract.—The larval development of *Symphurus williamsi* Jordan and Culver, 1895 (Cynoglossidae: Pleuronectiformes) is described from 69 specimens from the Gulf of California, Mexico. Diagnostic characteristics used to identify larvae of this species are 3–5 pigment spots situated on the dorsal region of the body of the base of the pterygiophore of the dorsal fin and 3–4 pigment spots on the ventral region of the body on the base of the pterygiophore of the anal fin. In early stages, a pigment is present on the base of each anal-fin ray. These pigments also appear at the bases of the dorsal-fin rays in the posterior third of the dorsal fin. The first three dorsal-fin rays are elongated in larvae less than 11.2 mm body length.

Symphurus is a world-wide genus distributed predominantly in temperate and tropical seas and oceans. The genus has 71 recognized species, 17 of which are found in the American region of the Pacific Ocean (Munroe, 1992). Thirteen species have been found in the Gulf of California: *S. atramentatus*, *S. atricaudus*, *S. callopterus*, *S. chabanaudi*, *S. elongatus*, *S. fasciolaris*, *S. gorgonae*, *S. leei*, *S. melanurus*, *S. melasmatotheca*, *S. oligomerus*, *S. prolatinaris*, and *S. williamsi* (Munroe and Mahadeva, 1989; Munroe, 1990; Munroe and Nizinski, 1990; Mahadeva and Munroe, 1990; Munroe et al., 1991; Munroe et al., 1995). Specimens of *Symphurus* are usually captured in large quantities by shrimp trawls in some tropical regions, but they are not exploited commercially because of their relatively small size (Pérez and Findley, 1985; Van der Heiden, 1985; Van der Heiden et al., 1986).

The taxonomy of the eastern Pacific species was poorly defined until the recent study of Munroe (1992), who concluded that it was possible to identify each of these species by a combination of the dorsal-, anal-, and caudal-fin ray counts and by the interdigitation patterns of dorsal proximal pterigyophores and neural spines (ID pattern).

Symphurus williamsi Jordan and Culver, 1895, can be found from the southern region of the Gulf of California, Mexico, to Panama in shallow waters with sandy bottoms (Munroe et al., 1995). Larvae occur throughout the Gulf of California. Large numbers were found during the summer in collections made south of Islas Tiburón and Angel de la Guarda (Aceves, 1992).

Of all species found in the American region of the Pacific, only the larvae of *S. atricaudus* (the only species of this genus distributed north as far as California) and *S. elongatus* have been described (Moser, 1981; Ahlstrom et al., 1984; Matarese et al., 1989; Charter and Moser, 1996). In this study, we offer a description of the larval stages of *S. williamsi* from preflexion through prejuvenile stages. Observations made on the larval development of *S. williamsi* are compared with those made previously on *S. atricaudus* and *S. elongatus*.

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Table 1

Meristics for species of *Symphurus* of the Gulf of California with the same pterygiphore interdigitation pattern (1-5-3-2-2) taken from Munroe (1992).

	S. williamsi	*S. atricaudus*	*S. chabanaudi*	*S. elongatus*	*S. melasmatotheca*	*S. melanurus*	*S. prolatinaris*
Dorsal-fin rays	89–95	94–102	98–109	99–107	90–98	96–104	103–110
Anal-fin rays	73–79	77–83	82–92	83–90	74–80	79–87	86–93
Caudal-fin rays	12	12	12	12	11	12	12
Total vertebrae	47–51	50–53	52–57	53–56	49–52	50–54	54–58

Materials and methods

Plankton samples were taken during eight oceanographic expeditions made in the Gulf of California in April, July–August, and November–December 1984, June and August 1986, July 1991, September 1993, and June 1994. Samples were obtained by using oblique tows with 60-cm diameter bongo nets equipped with nets of 333-µm and 505-µm mesh, as detailed in Kramer et al. (1972). All larvae and juveniles used in this study were deposited in the larval fish collection of the Plankton and Marine Ecology Department of Centro Interdisciplinario de Ciencias Marinas of the Instituto Politecnico Nacional (CICIMAR-IPN).

All *Symphurus* larvae collected with the 505-µm net were separated from the other net contents. Flexion, postflexion, and juvenile specimens were cleared, stained (Potthoff, 1984), and identified on the basis of meristic characteristics (Munroe, 1992). Subsequently, a developmental series of preflexion larvae showing similar pigmentation patterns and meristic features was assembled. Counts of the dorsal- and anal-fin elements were sometimes extrapolated from pterygiophore counts, which occasionally appeared earlier in development than did corresponding rays. The following measurements were done on the left side of the body of the specimens:

Body length (BL): anterior end of snout to end of notochord in young larvae, or to posterior margin of hypural plate in more developed larvae.

Head length (HL): anterior end of snout to cleithral margin in small specimens, or to posterior margin of the opercle in larger ones.

Snout-anus length (Sn-A): anterior end of snout to posterior margin of anus.

Body depth (BD): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of pelvic fin.

Body depth at anus (BDA): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of anal fin.

Eye diameter (ED): horizontal distance between anterior and posterior margins of left eye (Moser, 1996).

The description of larval development was based on 69 specimens (2.2–13.2 mm BL). None of these larvae were in the yolksac stage, indicating that eclosion must have taken place at a smaller size. To characterize larval development intervals, divisions proposed by Ahlstrom et al. (1976) were followed.

Results

Cleared and stained larval and prejuvenile specimens (n=17, between 7.7–13.2 mm BL) showed the following pterygiophore patterns: 1-5-3-2-2 (41.2%), 1-5-2-3-2 (35.2%), 1-5-2-2-2 (11.8%), 1-4-2-2-2 (5.9%), and 1-5-4-2-2 (5.9%). There are seven species in the area with the same main pterygiophore pattern (Table 1). Using these 17 specimens and the remaining 52 larvae (Table 2), we counted 9 precaudal vertebrae, 38–42 caudal vertebrae (mode=40), 89–97 dorsal rays (mode=92 and 94), 71–80 anal rays (mode=75), and 12 caudal-fin rays. The combination of these characteristics indicates that the species is *S. williamsi*.

Description of the larvae

Diagnosis *Symphurus williamsi* larvae typically have a pigmentation pattern of 5 spots along the middorsal line at the bases of the dorsal-fin pterygiophores and 2 to 3 similar spots located on the bases of the dorsal-fin rays. There are also 3 to 4

Table 2

Symphurus williamsi larvae and juvenile measurements (mm): body length (BL), snout-anus length (Sn-A), head length (HL), eye diameter (ED), body depth (BD), body depth at anal fin (BDA), and individual counts: dorsal rays (DR), anal rays (AR), caudal rays (CR), caudal vertebrae (CV), and total vertebrae (TV). Start of flexion stage (═══); start of postflexion stage (- - -); start of juvenile stage (——).

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
2.2	1.1	0.6	0.2	0.5	0.3				22	31
2.4	1.1	0.6	0.2	0.5	0.3				37	46
2.6	1.1	0.6	0.2	0.7	0.3				32	41
2.8	1.2	0.7	0.2	0.9	0.6				38	47
2.8	1.2	0.7	0.2	0.8	0.4				34	43
2.9	1.3	0.7	0.2	0.9	0.7				40	49
3.1	1.5	0.8	0.2	1.1	0.7				38	47
3.2	1.4	0.9	0.2	1.2	0.8				39	48
3.3	1.7	1.1	0.2	1.4	1.1				38	47
3.5	1.5	0.9	0.2	1.1	0.7				40	49
3.7	1.5	1.1	0.2	1.3	0.9				40	49
3.8	1.8	1.1	0.2	1.2	0.9				38	47
4.0	1.9	1.2	0.2	1.3	0.9				38	47
4.1	1.9	1.3	0.2	1.4	1.1				40	49
4.3	1.9	1.1	0.3	1.6	1.2				40	49
4.3	1.9	1.1	0.3	1.6	1.1				40	49
4.5	2.1	1.2	0.2	1.8	1.1				41	50
4.6	2.0	1.3	0.2	1.5	1.2				40	49
4.8	1.8	1.1	0.2	1.5	0.9				39	48
5.0	2.0	1.2	0.3	1.7	1.4				39	48
5.0	1.9	1.2	0.2	1.7	1.1				40	49
5.0	2.1	1.3	0.3	1.6	1.2				38	47
5.3	2.1	1.4	0.3	1.7	1.2				40	49
5.6	2.0	1.4	0.3	1.5	1.1				41	50
5.8	2.3	1.5	0.3	1.9	1.4				40	49
5.9	2.3	1.4	0.3	1.9	1.2				40	49
6.1	2.4	1.6	0.3	1.9	1.5				40	49
6.1	2.2	1.7	0.3	1.9	1.4		80		40	49
6.3	2.4	1.5	0.3	1.8	1.4				40	49
6.6	2.2	1.6	0.3	2.1	1.5				38	47
6.8	2.5	1.7	0.3	2.3	1.5	92	79		41	50
7.0	2.6	1.6	0.3	1.9	1.5	92	77		41	50
7.2	2.7	1.8	0.3	2.2	1.7	92	75		40	49
7.3	2.7	1.7	0.3	1.9	1.5	95	79		40	49
7.4	2.5	1.7	0.3	2.3	1.5	94	75		41	50
7.7	2.6	1.7	0.3	2.0	1.7	92	75	12	40	49
7.8	2.9	1.9	0.3	2.0	1.6	94	76	12	38	47
8.0	2.8	2.0	0.3	2.2	1.7	93	77		41	50
8.2	2.8	1.9	0.3	2.3	1.9	96	77	12	40	49
8.3	3.1	2.0	0.3	2.4	1.9	95	76	12	41	50
8.3	2.9	1.9	0.3	2.4	1.8	96	79	12	40	49
8.3	2.9	1.9	0.3	2.3	1.9	93	76	12	40	49
8.4	3.0	1.9	0.3	2.1	1.5	94	76	12	39	48
8.7	2.9	2.2	0.3	2.5	2.1	91	74	12	40	49
9.3	3.0	2.1	0.3	2.0	1.6	94	75	12	38	47
9.5	3.3	2.2	0.3	2.3	2.0	94	77	12	40	49
9.6	3.4	2.2	0.3	2.6	2.1	91	75	12	38	47
9.8	3.1	2.0	0.3	2.3	2.0	92	76	12	40	49
9.9	3.2	2.1	0.3	2.2	2.0	93	71	12	39	48
9.9	3.2	2.1	0.3	2.3	2.1	94	78	12	41	50
10.0	3.0	2.2	0.3	2.5	2.2	91	75	12	40	49
10.2	2.8	2.2	0.3	2.4	2.2	92	75	12	41	50

continued

Table 2 (continued)

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
10.4	3.1	2.2	0.4	2.5	2.3	92	76	12	41	50
10.6	3.4	2.3	0.4	2.3	2.1	93	74	12	38	47
10.6	3.3	2.3	0.3	2.2	2.2	91	75	12	39	48
10.7	3.5	2.2	0.3	2.6	2.3	94	76	12		
10.8	3.3	2.5	0.4	2.6	2.4	91	73	12	39	48
11.1	3.4	2.4	0.3	2.5	2.2	94	77	12	39	48
11.1	3.6	2.5	0.3	2.7	2.7	90	75	12	38	47
11.1	3.7	2.6	0.3	2.4	2.4	97	80	12	39	48
11.1	3.7	2.5	0.3	2.4	2.4	93	76	12	42	51
11.3	3.5	2.5	0.3	3.0	2.3	92	77	12	39	48
11.4	3.3	2.3	0.3	2.5	2.3	94	79	12	40	49
11.7	3.4	3.2	0.4	3.5	3.3	93	73	12		
11.9	3.8	2.8	0.3	2.5	2.3	92		12	40	49
12.7	3.2	2.5	0.4	2.3	2.7	91	75	12	38	47
12.9	3.9	3.0	0.3	2.4	2.6	89	74	12	39	48
13.1	3.9	3.0	0.3	3.1	2.4	94	74	12		
13.2	3.4	2.9	0.3	2.2	2.9	92	75	12	39	48

spots along the midventral line at the bases of the anal-fin pterygiophores, and 1 to 2 similar spots located on the anal-fin ray bases. At time of formation of the anal-fin rays, a melanophore appears at the base of each fin ray. A similar pigment is also found at the base of each dorsal- fin ray in the posterior third of the body in larvae less than 11.2 mm BL. The first 3 dorsal rays are elongated in larvae less than 11.2 mm BL, with the second and third of these longer than the first.

Morphological features The body is compressed and ribbonlike and has a deep head. The gut extends beyond the ventral profile. The intestine is noticeably coiled and its terminal end is directed towards the right side of the body. Larvae attain the appearance of juveniles when the protruding gut is incorporated within the ventral body profile at approximately 12 mm BL. At metamorphosis, a fleshy rostral beak is formed anterior to the dorsal-fin origin.

Migration of the right eye starts at 6.1 mm BL and eye migration is completed in larvae of 11.1 mm BL. The migrating eye crosses anterior to the dorsal-fin origin, between the rostral beak and the interorbital region. Notochord flexion begins at 5.0 mm BL and is completed near 8.0 mm BL. The juvenile stage begins at about 11.9 mm BL (Table 2).

Growth is not isometric throughout larval development (Table 3). Head length, snout-anus length, and body depth decrease with respect to body length from preflexion to juvenile stages. Body depth at the anal-fin origin remains constant throughout development. Eye diameter in relation to head length decreases from preflexion to juvenile stages.

Table 3

Symphurus williamsi larvae and juvenile body proportions (in percent of BL): body length (BL), head length (HL), snout-anus length (Sn-A), body depth (BD), body depth at anal fin (BDA), and eye diameter (ED).

Body proportions	Average	Standard deviation	Interval
HL:BL			
Preflexion	27	2.8	23–33
Flexion	25	1.3	23–28
Postflexion	23	1.5	20–27
Juvenile	22	1.4	20–24
Sn-A:BL			
Preflexion	45	3.3	38–52
Flexion	38	2.2	33–42
Postflexion	33	2.4	28–37
Juvenile	29	2.6	25–32
BD:BL			
Preflexion	33	5.2	21–42
Flexion	31	2.5	26–34
Postflexion	25	2.6	21–30
Juvenile	20	2.5	17–24
BDA:BL			
Preflexion	22	5.5	12–33
Flexion	23	2.0	20–28
Postflexion	22	2.0	17–28
Juvenile	20	1.3	18–23
ED:HL			
Preflexion	24	6.2	15–33
Flexion	19	2.5	15–25
Postflexion	14	1.8	12–18
Juvenile	11	2.3	10–12

Formation of scales begins at 7.7 mm BL over the cephalic region, and by about 10.3 mm BL, scales are evident over the entire body.

Pigmentation Early preflexion larvae typically have three melanophores along the middorsal line and two or three on the dorsal-fin fold. Three other melanophores are present along the midventral line, and one or two similar spots are found on the anal-fin fold. A melanophore is located over the coiled intestine in anterior and posterior positions. The ventral surface of the coiled intestine shows numerous smaller and dispersed melanophores. Two other melanophores appear in the anterior region: one on the cleithrum near the base of the pectoral bud; the other on the ventral margin of the preopercle. The dorsal surface of the swimbladder is also pigmented (Fig. 1A).

With finfold disappearance (late preflexion larvae), the characteristic pigmentation pattern is established: five spots located along the middorsal line at the bases of the dorsal-fin pterygiophores and two or three spots on the bases of dorsal-fin rays. Three or four spots appear along the midventral line at the bases of the anal-fin pterygiophores, and one or two spots are present on the bases of anal-fin rays.

When formation of the dorsal- and anal-fin rays is complete, a pigment spot appears on the base of each anal ray. Similar pigments are found on the bases of the fin rays in the posterior third of the dorsal fin. On the head, an inner melanophore appears over the forebrain and another over the otic region. Finally, a melanophore is present on the distal margin of the peduncle of the pectoral fin (Fig. 1B).

During the flexion stage, the pigmentation pattern of preflexion larvae remains, but the spots on the bases of anal- and dorsal-fin rays sometimes disappear. The pigment over the otic region, that on the opercle margin, and the melanophore on the posterior part of the intestine also disappear. In this stage there are additional pigments that appear. A series of dots are found over the ventral margin of the head, and a melanophore appears over the inferior portion of the base of the ventral fin. Flexion larvae are similar to those of postflexion larvae (Fig. 2A).

At the postflexion stage, three melanophores appears on the bases of the caudal-fin rays, and at 11.2 mm BL, the cephalic and opercular pigments may disappear (Fig. 2A).

In early juveniles, four spots appear on the midline of the body. Their positions with respect to the melanophores already present on the dorsal margin are one between second and third spots, one between third and fourth, one directly ventral to the fourth spot, and one posterior to the fourth spot. There is now pigment on the base of every dorsal-fin ray throughout the entire fin. A series of small spots also develop on the rays on the anterior part of the anal fin (Fig. 2B).

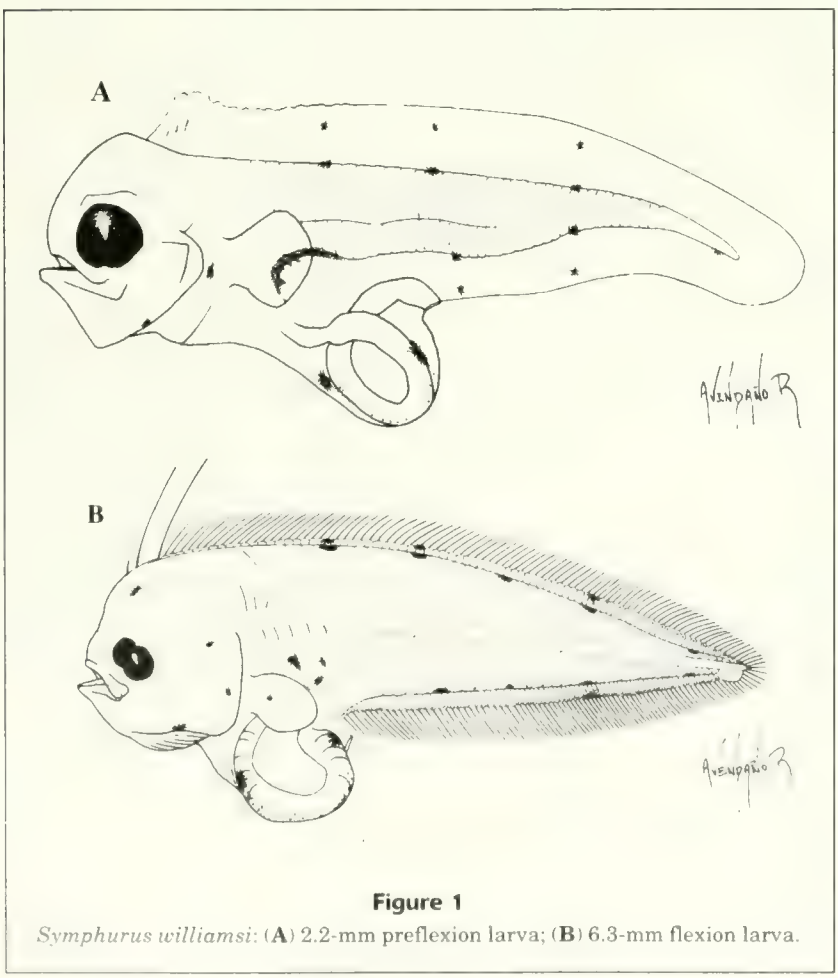

Figure 1

Symphurus williamsi: (**A**) 2.2-mm preflexion larva; (**B**) 6.3-mm flexion larva.

Fin formation

Unpaired fin development Incipient dorsal-fin rays are present in the anterior dorsal finfold at 2.8 mm BL. At 4.0 mm BL, about one half of the dorsal and anal rays are formed in a posterior direction. Complete formation of these fins occurs at about 6.8 mm BL. The 3 elongated dorsal-fin rays, present since this fin originated, disappear at 11.4 mm BL.

Paired fin development Pectoral-fin buds are present in the smallest lar-

vae we have seen (2.2 mm BL). This fin is reabsorbed at the postflexion stage (10.3 mm BL). Pelvic fins are developed at 5.7 mm BL. Only in early juveniles is a blind-side pelvic fin located on the midventral line and the ocular pelvic fin is in a more dorsal position.

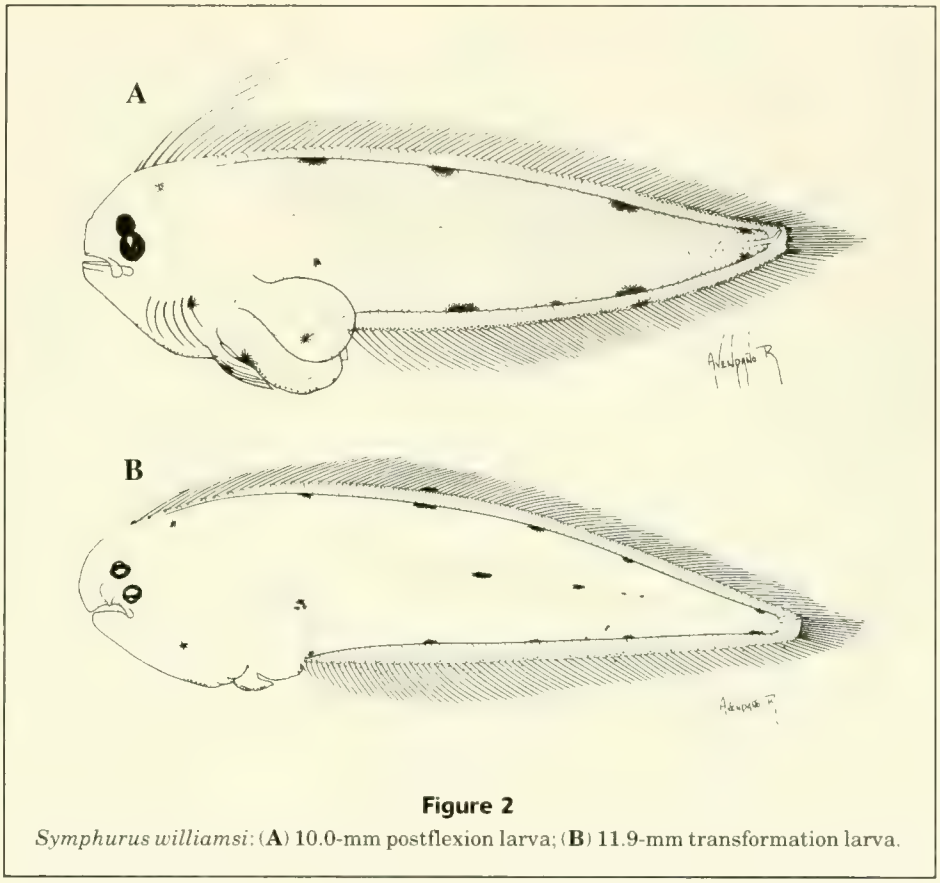

Figure 2
Symphurus williamsi: (**A**) 10.0-mm postflexion larva; (**B**) 11.9-mm transformation larva.

Discussion

Larvae of *S. williamsi* are easily distinguishable from those of *S. atricaudus* by differences in pigmentation patterns. During early preflexion stage, *S. williamsi* has two or three pigments over the dorsal and midventral lines, and the pigments over the finfold are in the middle. *S. atricaudus* has a series of small melanophores along the midventral line. The pigments over the finfold are in blotches and are on the ventral and dorsal margins. There are also several pigments over the ventral margin of the head and the gut that *S. williamsi* does not have.

At the flexion stage, *S. williamsi* has the spot pattern along the dorsal and ventral profile. In contrast, *S. atricaudus* has a series of melanophores along the dorsal- and anal-fin margins and a series of pigments along the midbody line that never develop in *S. williamsi*.

In *S. williamsi*, three elongated rays are characteristic. In *S. atricaudus*, five rays appear first in the dorsal fin but never become elongated. The intestine in *S. williamsi* projects only ventrally, whereas in *S. atricaudus* the projection is ventroposterioriad.

Larvae of *S. williamsi* can be distinguished from those of *S. elongatus* by the pigmentation patterns. In the preflexion stage, *S. elongatus* does not have spots at the bases of the dorsal-fin rays, and these larvae do not have pigments at the bases of each of the anal- and dorsal-fin rays. Later in their development, the pigmentation of *S. elongatus* consists of a few distal pigments on the anal fin, twelve dashes along the lateral midline, and a small blotch on the caudal-fin rays, not observed in *S. williamsi*. In the early transformation stage, *S. elongatus* has a series of melanophores over the anterior part of the head, which never appear in *S. williamsi*. Like *S. atricaudus*, *S. elongatus* never develops elongated rays.

Yevseyenko (1990) described *Symphurus* sp. larvae. Its meristic characters have led us to believe it is *S. callopterus*, principally because of its ID pattern. These larvae are different from those of *S. williamsi* in pigmentation pattern because on the caudal section of the body an accumulation of pigment in the form of two oblique bands and two belts are found. These pigments are approximately equidistant from one other and never are found in *S. williamsi*.

Instead of three elongated dorsal-fin rays, like *S. williamsi*, *Symphurus* sp. have the first 7 dorsal-fin rays elongated from 7.5 to 25.4 mm BL (Yevseyenco, 1990). The presence of elongated fin rays in pleuronectiform larvae has phylogenetic interpretations only in bothids and appears to be apomorphic within the order and this family (Hensley and Ahlstrom, 1984). However the use of this characteristic for phylogenetic interpretations in cynoglossids does not allow proper comparisons because most larvae remain unknown.

Adults of *S. williamsi* (7.5 to 11.6 cm BL) are smaller than those of *S. atricauda* (13 to 18 cm BL)

and *S. elongatus* (13.5–15 cm BL) (Munroe et al., 1995), and this size difference is observed in larvae also. All stages of development in *S. williamsi* occur at smaller sizes (flexion between 5.0 and 8.0 mm and transformation >11.9 mm) than in other species. The flexion stage in *S. atricaudus* occurs between 8.6 and 10.8 mm BL (Ahlstrom et al., 1984; Matarese et al., 1989), and the transformation stage between 19 and 24.2 mm BL (Kramer, 1991). The flexion stage in *S. elongatus* is >6.8 mm and <18.9 mm BL and transformation takes place from >18.9 mm to <28.3 mm BL (Charter and Moser, 1996). In *Symphurus* sp. transformation occurs between 21 and 38 mm BL (Yevseyenko, 1990).

Usually the size range at metamorphosis that is plesiomorphic for the order is ca. 10 to 25 mm BL because most pleuronectiforms metamorphose in this range (Hensley and Ahlstrom, 1984).

Metamorphosis in *S. williamsi* occurs at ca. 11.9 mm BL; however, as described by Hensley and Ahlstrom (1984), size at metamorphosis is an important characteristic for larval identification, but its use for inferring phylogenetic relations in most instances is premature.

Symphurus williamsi has a larger head at all developmental stages, compared with those of *S. atricaudus* and *S. elongatus*. The distance from snout to anus in *S. williamsi* is relatively longer than it is in *S. atricaudus* but is similar to that of *S. elongatus*. In the juvenile stage, this distance is longer in *S. williamsi* than it is in *S. elongatus*. Larvae of *Symphurus* sp. as described by Yevseyenko (1990) have an abdominal cavity extending downward. This projection has the form of a greatly elongated sac, and the lower end terminates in a wormlike process that *S. williamsi* does not have. The loop of the intestine in *Symphurus* sp. is almost one half of the body length.

The body depth at the preflexion stage is greater in *S. williamsi* compared with that in *S. atricaudus* but is similar to that of larvae of *S. elongatus*. In postflexion and prejuvenile stages, this proportion is smaller in *S. williamsi* than in both of these other species.

Finally, body depth at the anus is shallower in *S. williamsi* than it is in *S. elongatus* at all stages in *S. atricaudus* during flexion and juvenile stages.

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Catchability estimates and their application to the red grouper (*Epinephelus morio*) fishery of the Campeche Bank, Mexico

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Abstract.—We applied a length-based additive catchability model that accounts for several sources of variation, namely time (i.e. years, months), density-dependence effects, and different fishing fleets. The model is based on 1) a transition matrix and 2) population length-structured data expressed as catch per unit of effort. Other sources of variation were estimated as anomalies from the average pattern and incorporated as additions to the slope of the catchability-at-length equation. The catchability model was applied to the red grouper (*Epinephelus morio*) fishery of the north continental shelf of Yucatan, a demersal fish resource exploited by three different fleets. A sigmoidal shape catchability-at-length function was fitted on the basis of grouper population biology and behavior, particularly reproductive aggregation. Catchability of immature fish was constant but increased with size for adult fish, especially during the reproductive season. Time- and density-dependent catchability responded to reproductive behavior and the allocation of fishing effort. When differences between fleets were incorporated, catchability differences emerged. The catchability model has the ability to identify the main properties of the fish resource and fishery that affect the relation between fishing effort and population abundance; it may therefore be helpful as an alternative stock assessment tool.

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Catchability has been considered in fisheries science as a parameter in the catch equation that relates fishing effort to population abundance:

$$C = qsEN, \quad (1)$$

where C = catch in numbers;
q = catchability;
s = probability of gear selection;
E = fishing effort; and
N = the stock size in numbers.

From this relation it is easy to understand the key role of q. Because s and E are controlled by man, changes in population abundance will be reflected in catch through q. Although classically considered a constant, q represents different sources of variation affecting stock size. Most of the existing catchability models deal with only one source of variation related to schooling of fish (e.g. MacCall, 1976; Csirke, 1988, 1989), although a few of them also consider environmental factors (Table 1).

Investigations on catchability have developed mainly in two directions (Arreguín-Sánchez, 1996): 1) those related to measuring and increasing gear efficiency, and 2) those that use catchability as a parameter to relate fishing effort to fishing mortality and population abundance for stock assessment and management purposes. The aim of this contribution is to apply a catchability model that accounts for several sources of variation related to fishing and to population processes, as proposed by Arreguín-Sánchez (1996).

The red grouper (*Epinephelus morio*) stock over the Campeche Bank is one of the largest in the world, distributed on a continental shelf of more than 100,000 km^2. As with many serranids, the red grouper stock over the Campeche Bank, Gulf of Mexico, aggregates for reproduction, a fact that is well documented in the literature (Arreguín-Sánchez et al., 1996). While they aggregate, these fish are highly vulnerable to fishing; therefore this fish behavior is a key aspect for management of the resource. Three fleets target this fish species: two from Mexico (an artisanal and a midsize fleet); and a third from Cuba. These fleets do not completely overlap in respect to their fishing grounds, and their catch structure, efficiency, and the fishing mortality that they cause to the stock are different. Our contribution is aimed to estimate catchability for the red grouper fishery.

Table 1

Catchability models in literature accounting for more than one source of variation.

Catchability model	Comments	Reference
$q_t = q_0 exp^{rt}$ $r_t = \alpha_1 (t)$ $r_2 = \alpha_2 E(t)$	t=time, E= fishing effort	Quinn (1987)
$q = 0.085\ N^{-0.384}$ $q = 0.287\ N^{-0.278}$	Haddock, George's Bank N = population abundance *Area* = population habitat	Grecco and Overholtz (1990)
$q = 0.095\ N^{-0.787}$ $q = 0.003\ Area^{-0.747}$	Cod gill net, Atlantic B=Stock biomass *Area* = population habitat	Rose and Legget (1991)
$q = q_1 \frac{T\ q_2}{1 + q_3 B_t}$	Peruvian anchoveta. q_1 = base fraction of the stock size per unit of effort (when stock size is low); B = biomass; T = temperature; q_2 and q_3 are constants	Hilborn and Walters (1992)
$q(\ell, t, E, F) = f$(size)	ℓ = length, t = time, E = fishing effort; f = fleets	Arreguín-Sánchez (1996)

Materials and methods

We assume that catchability 1) is length dependent; 2) depends on fish behavior; 3) and is density dependent. For fishing effort, we also assume that 1) these assumptions can be valid for individual fishing fleets, such that we can explicitly consider the individual contribution of the several fleets participating in the fishing process and 2) that units of effort have static properties, that is to say, a consistent fishing power over time.

Length-dependent catchability

The catchability coefficient must be estimated for each length class in a given time, $q(\ell,t)$. A convenient form to represent the transformation of one length-frequency distribution (representing the structure of the stock) into another is by means of a transition matrix (Shepherd, 1987; Caswell, 1988), so that

$$N(\ell, t+1) = A(\ell, k) N(\ell, t), \qquad (2)$$

where k and ℓ = successive length intervals;
$N(\ell,t)$ = is the stock size in numbers at time t; and
A = the transition matrix that depends on growth and mortality.

Although these processes occur concurrently, Shepherd (1987) assumed that they can be separated as the product of two terms:

$$A(\ell, k) = G(\ell, k) S(k),$$

where G = the effect of growth in absence of mortality; and
S = the effect of mortality (survival) and also of selection of the sampling gear.

Matrix $G(\ell,k)$ can be easily estimated by following the criteria defined by Shepherd (1987) to assign growth probabilities to each length class. The elements of $S(k)$can be defined in terms of mortality as

$$S(k) = e^{-Z(k)t} = e^{-[M + q(k)t + s(k)E(t)]},$$

where $S(k)$ represents the values of the elements in the main diagonal of the survivorship matrix (other elements are zero; see Caswell, 1988); $Z(k)t$ is the instantaneous rate of total mortality for the k^{th} length group at time t; M is the instantaneous rate of natural mortality (assumed constant); $s(k)$ is the probability of gear selection for length k; and $E(t)$ is the fishing effort at time t (which is assumed nontargeted to specific sizes within a range of sizes captured by the gear). Then fishing mortality is given as $F(k, t) = q(k, t)\ s(k)E(t)$.

Equation 2 can therefore be represented as

$$N(\ell, t+1) = \sum_k G(\ell, k) e^{-[M + q(k,t) + s(k)E(t)]} N(k,t). \qquad (3)$$

If $N(\ell t+1)$, $N(k,t)$ and $G(\ell,k)$ are known, as well as M, $s(k)$, and $E(t)$, then $q(k,t)$ can be estimated. Equation 2 can then be solved iteratively for $q(k,t)$ by using an algorithm to minimize differences between observed and calculated values of $N(\ell, t+1)$.

Once $q(k,t)$ values are obtained, the catchability pattern with length can be observed and a tendency

quantified. Although a catchability-at-length model may be empirically determined, its interpretation must be made by considering the population biology and behavior of the fish. On an annual basis, the model is represented by the function

$$q(\ell)\alpha\beta(\ell)\cdot\ell \tag{4}$$

whose slope $\beta(\ell)$ represents the rate of change of catchability with length for a given year. If several years are considered for a stable period of the fishery, then a general function can be estimated where the slope of the length-based catchability pattern in Equation 4 can be expressed by $\beta(\ell,\bullet)$, where the symbol $\bullet$ represents the average stock level over a range of years in which it can be reasonably assumed to be stable.

Time-dependent catchability

Gulland (1983) expanded the scope of the catchability coefficient to a structured population as expressed in the following equation:

$$C(\ell,\Delta t) = q(\ell,\Delta t)s(\ell)E(\Delta t)N(\ell,\Delta t). \tag{5}$$

This represents the capture of fish of various sizes (ℓ) during a time period Dt. Taking the mean stock size ($\bar{N}$), and rewriting Equation 5 in terms of catch per unit of fishing effort, U, we obtain

$$U(\ell,\bullet) = q(\ell,\bullet)\bar{N}(\ell),$$

with $$U(\ell,\bullet) = C(\ell,\Delta t)/s(\ell)E(\Delta t)$$

and then

$$\begin{aligned}\mathrm{Ln}\left[U(\ell,t)/U(\ell,\bullet)\right] &- \mathrm{Ln}\left[q(\ell,t)\bar{N}(\ell)/q(\ell,\bullet)\bar{N}(\ell)\right] \\ &= \mathrm{Ln}\left[q(\ell,t)/q(\ell,\bullet)\right].\end{aligned} \tag{6}$$

This can be interpreted as the departure or anomaly in catchability at time t with respect to the average for a given length class. Arreguín-Sánchez (1996) suggested that this ratio is a linear function of size, represented by the midlength class as

$$\mathrm{Ln}\left[q(\ell,t)/q(\ell,\bullet)\right] = \alpha(t) + \beta(t)\ell, \tag{7}$$

where

$$\beta(t) = \mathrm{Ln}\left[q(\ell+1,t)/q(\ell,t)\right] - \mathrm{Ln}\left[q(\ell+1,\bullet)/q(\ell,\bullet)\right].$$

The intercept $\alpha(t)$ in Equation 7 can be interpreted as the relative vulnerability of small fish, and also as an index of the relative abundance of recruits. The slope $\beta(t)$ expresses the rate of change of catchability-at-length with respect to the average, or in other words, the departure (anomaly) from the average catchability pattern with length.

Once $\beta(\ell,\bullet)$ is estimated from Equation 4, the value of $\beta(t)$ can be added to $\beta(\ell,\bullet)$ to obtain the corresponding catchability values for a given time period.

Amount of fishing and density-dependent catchability

The relation between population size and catchability has been most studied in pelagic clupeoid fish (Murphy, 1966; MacCall, 1976; Csirke, 1988, 1989; Pitcher, 1996), where catchability is inversely related to stock size. Thus a density-dependent effect can be approached by considering the population as a whole, and the function

$$\bar{q}w(t) = f\{N(t)\} \tag{8}$$

can be fitted, where $\bar{q}w(t)$ is the weighted value of q at time t, with U at time t as a weighting factor. An analogous approach is proposed for each length class. For a stable period of time, we can assume that the amount of fishing, or the total fishing effort E, is one of the main sources of variation of the population density and the structure of the exploited stock. A change in both of these population characteristics will be reflected in the $\beta(t)$ coefficient. With Equations 1 and 8, it is possible to relate changes in $q(\ell,t)$ as a function of coefficient $\beta(t)$:

$$\beta(t)\alpha\,\beta(E)\cdot\ell, \tag{9}$$

where a constant natural mortality rate is assumed for all length classes over time.

Because $\beta(t)$ represents the departure of the catchability pattern with length at time t, Equation 9 measures the effect of the amount of fishing on the anomaly, and it is represented by the slope $\beta(E)$. The magnitude and sign of $\beta(E)$ will provide information about changes in stock density. A negative sign means that for a low level of fishing, q will increase with fish length.

Catchability differences between fleets

Following the same rationale as that in Equation 7, differences in q between fleets as a function of length can be estimated. If q and h represent two different fishing fleets, Equation 6 can now be expressed as

$$\mathrm{Ln}\left[U(g,\ell,t)/U(h,\ell,t)\right] = \mathrm{Ln}\left[q(g,\ell,t)/q(h,\ell,t)\right] \tag{10}$$

and

$$\mathrm{Ln}[q(g,\ell,t)/q(h,\ell,t)] = \alpha(f) + \beta(f)\cdot\ell, \qquad (11)$$

where f indexes fishing fleets.

In this case, the intercept $\alpha(f)$ is the relative difference in catchability between fleets for the smallest fish. The slope $\beta(f)$ reflects the difference in fishing performance measured as the anomaly in catchability of the fleet g with respect to the fleet h.

The additive catchability model

The deterministic model that incorporates the processes discussed can now be set out. It relies on the changes of the slope $\beta(\ell, \bullet)$, representing the catchability-at-length pattern, by the addition of the slopes of the partial effects described by Equations 7, 9, and 11. The slope of the catchability model, with the form defined by Equation 4, is represented by

$$\beta(\ell,t,E,f) = \beta(\ell,\bullet) + \beta(t) + \beta(E) + \beta(f). \qquad (12)$$

The value of $\beta(\ell, t, E, f)$ represents the slope of the catchability-at-length function without restriction to equilibrium, which has been compensated by the addition of the term $\beta(t)$, where t refers to any appropriate unit of time.

The red grouper (*Epinephelus morio*) fishery in the Campeche Bank, Mexico

The red grouper on the North continental shelf of Yucatan is exploited by three fleets: an artisanal and a mid-size fleet from Mexico, and a large-scale fleet from Cuba. These fleets overlap in respect to their fishing grounds (Moreno et al.[1]): Mexican fleets overlap in a range of 60% to 70%; the midsize fleet from Mexico and large-scale fleet from Cuban, around 60%; and the artisanal and Cuban fleets, between 12% and 16%. This overlap in fishing grounds means that each fleet causes fishing mortality on different sizes of the stock and thus necessitates that the fleets be considered separately for stock assessment purposes.

The artisanal fleet of Mexico is composed of vessels of approximately 9 m long, operating from the coast to 20 m depth, and catching mainly juvenile and preadult fish. The midsize fleet uses 15-m vessels operating at depths of 10 to 80 m, and catch comprises both juvenile and adult fish, according to the season. The Cuban fleet fishes mainly with 27-m vessels, operates between 20 and 90 m depth, and catches adult fish. Both Mexican fleets have free access and move seasonally in the area following changes in fish density (i.e. with reproductive aggregation). The Cuban fleet has a catch quota of 3900 t of demersal fish, of which more than 80% is red grouper. This fleet remains in the central and eastern region of the continental shelf of Yucatan most of the time.

Differences related to gear, fishing effort, and fishing strategies among fleets are described in Moreno (1980), Burgos (1987), and Fuentes (1987) for the midsize fleet; Sáenz et al. (1987), Salazar (1988), and Solana-Sansores and Arreguín-Sánchez (1991) for the artisanal fleet; Valdés and Padrón (1980) for the Cuban fleet; and Seijo (1986), González-Cano et al. (1993), and Arreguín-Sánchez et al. (1996) for the three fleets. In this paper we used standardized fishing days as the unit of fishing effort.

For the catchability model, available data for the red grouper fishery are summarized in Table 2. Detailed information is derived from the midsize fleet, which harvests around 70% of the total annual yield. Other fleets share the remaining 30% more or less equally. Because the midsize fleet also catches a size range that overlaps the other two, this fleet is the start of our analysis. Later, we will incorporate the other fleets into the catchability model.

To solve Equation 3, we assumed that individual growth follows the von Bertalanffy equation with values of L_∞ = 87 cm total length (TL) and K = 0.12/year (Arreguín-Sánchez[2]), and the natural mortality coefficient M = 0.3/year (Doi et al., 1981; Contreras et al., 1994).

The selection factor for each length class $s(\ell)$, representing a probability term directly affecting the abundance of length classes in the catch, was set to be $s(\ell)$ = 1. For simplicity, red grouper fishery gears were assumed nonselective (hook-and-line and hand lines with different sizes and baits).

Annual catch-per-unit-of-effort(U)-at-length data for the period 1973 to 1987 for the midsize fleet was used. The iterative procedure described for Equation 3 was applied to each pair of yearly data to obtain initial values of catchability per length class and year. Catchability values for each length class $q(\ell, y)$ were used to fit the trend with length (Fig. 1) and to describe variability of $q(\ell, \bullet)$. The solution for Equation 3 does not require a previous knowledge of recruits at $U(\ell, t)$ and $U(\ell, t+1)$, and it was solved for

[1] Moreno, V., F. Arreguín-Sánchez, M. Contreras, and R. Burgos. 1991. Analysis of usage patterns in shared stocks: the red grouper fishery from the continental shelf of Yucatan, Mexico. Proc. 44th Ann. Sess. Gulf and Caribb. Fish. Inst., 18 p. [Mimeo.]

[2] Arreguín-Sánchez, F. 1996. Length-based growth estimation for the red grouper (*Epinephelus morio*) in the North continental shelf of Yucatan, Mexico. Centr. Interdiscip. Cienc. Mar., México, 19 p. [Manuscript.]

Table 2

Summary of the data used in this paper for the red grouper fishery on the north continental shelf of Yucatan, Mexico. Fleets operate with long lines of different sizes (artisanal also uses hook-and-line). Fishing effort was standardized as fishing days (see Arreguín-Sánchez et al., 1996)

Fleet	Annual catch-at-length	Monthly catch-at-length	Sampling design	Site of landing
Artisanal[1]	1987	1987	three stages (port, vessels, baskets)	Ports along the coast of Yucatan, Mexico
Midsize[2]	1975 to 1987 (except for 1986)	1975 to 1987 (except for 1986)	two stages (day/vessel and commercial size)	Port of Progreso, Mexico
Cuban fleet[2]	1975 to 1987		two stages (vessels and commercial size).	Port of La Havana, Cuba

[1] Source: Centro de Investigación y de Estudios Avanzados del IPN, Yucatan, Mexico.
[2] Source: Instituto Nacional de la Pesca, Centro Regional de Investigación. Pesquera de Yucalpetén, Yucatan, Mexico.

$n-1$ or $n-2$ catchability values, with differences in n caused by the absence of recruitment estimates. Because we fitted the general tendency as a catchability-at-length pattern, one or two missing points will not affect the estimates.

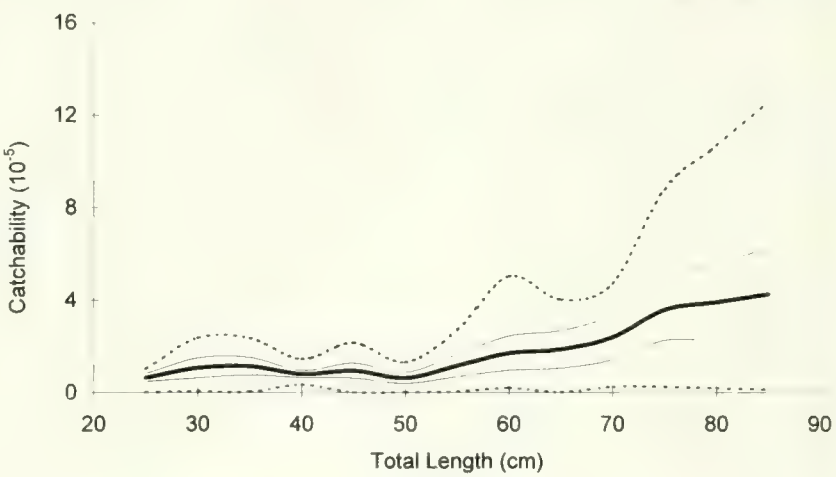

Figure 1

Catchability-at-length pattern for the Mexican midsize fleet of the red grouper fishery estimated with Equation 3. The bold line indicates average values over the period from 1973 to 1987; thin lines denote one standard deviation, dashed lines represent absolute minimum and maximum values.

Results

Length-dependent catchability

The fitting process required some consideration of population behavior because trend could be adjusted to an exponential or sigmoidal function. We decided on a sigmoidal form because of reproductive behavior. During reproductive aggregation, adult fish (>50 cm TL) form groups with a sex ratio (females: males) close to 6:1, comprising individuals of around the same size, but without any apparent size segregation between groups. This is well known by fishermen, and has been described by Moe (1969), Shapiro (1987), and Mexicano-Cíntora (1990). In terms of fishing, adults within a specific area have the same probability of catch. In the catchability-at-length trajectory, we think this reproductive behavior can be well represented by an asymptotic trend of catchability for large fish.

The variation in catchability of young fish, as expressed by one standard deviation (Fig. 1) was similar for lengths between 20 to 50 cm and increased sharply after first maturity (at 50 cm TL, as defined by Mexicano-Cíntora, 1990).

The generalized catchability-at-length equation fitted for the red grouper was

$$q(\ell,\bullet) = \frac{0.00004256}{1+e^{-3.8965+0.0064\ell}} \qquad (13)$$

with the standard error (SE) of the ordinate $SE\alpha = 0.773$, and $SE_\beta = 0.012$ for the slope; $R^2 = 0.728$ (df=10).

Time-dependent catchability

Time variation of catchability was analyzed considering both annual and monthly catch-structured data. From Equation 7, parameters $\alpha(y)$ and $\beta(y)$ were estimated by regressing

$$\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$$

with length (Fig. 2). Table 3 shows values of the constants for both midsize Mexican and Cuban fleets for annual data.

On a monthly basis, the same computations were developed for the mid-size fleet. Departures represented in parameters $\alpha(m)$ and $\beta(m)$ were estimated in a similar way to those in Equation 7, but considering annual catch-structured data. Seasonal changes in vulnerability occurred: q increased in winter (December to February) in synchrony with the reproductive aggregation (Fig. 3). Catchability was lower in autumn, when the population is dispersed along the continental shelf and the vulnerability of young fish in coastal waters increases.

Catchability differences between fleets

Following Equation 11, differences between fleets were evaluated by comparing annual data for the Cuban fleet with those of the mid-size fleet for the period 1975 to 1987. Mexican mid-size and artisanal fleets were compared on a monthly basis for 1987. Parameters for $\alpha(f)$ and $\beta(f)$ were obtained (Tables 4 and 5). Positive values of $\beta(f)$ indicate that relative catchability for small fish is higher for the midsize fleet than for the Cuban fleet; and lower for large fish. This scheme represents differences in fishing areas between fleets. The negative value $\beta(f)$ for in 1982 suggests fleets changed their usual behavior. Similar interpretation can be made for monthly data between the artisanal and mid-size fleets.

Figure 3 shows the tendency of

$$\mathrm{Ln}[U(\text{mid-scale},\ell,t)/U(\text{Cuban},\ell,t)]$$

with length. An inflection point is observed just at the length at first maturity (i.e. 50 cm LT). Positive values indicate that q is higher in small (immature) fish for the midsize fleet than for the Cuban fleet, whereas q is equal in both fleets for mature fish. For the tendency of

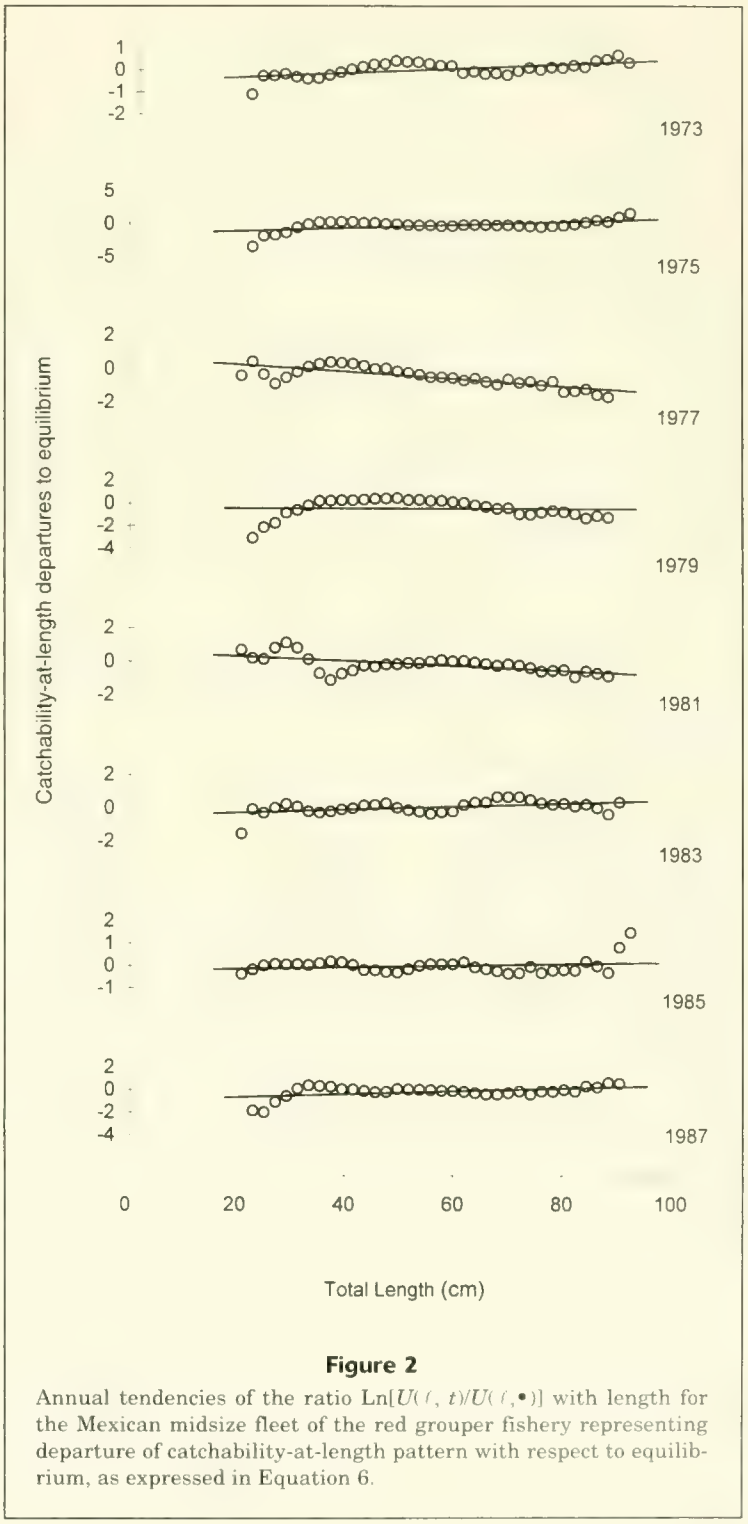

Figure 2

Annual tendencies of the ratio $\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$ with length for the Mexican midsize fleet of the red grouper fishery representing departure of catchability-at-length pattern with respect to equilibrium, as expressed in Equation 6.

$$\mathrm{Ln}[U(\text{artisanal},\ell,t)/U(\text{mid-scale},\ell,t)]$$

with length, catchability of immature fish was higher for the artisanal than for the midsize fleet, and again equal for adult fish up to 65 cm TL. For fish larger than 65 cm, q was higher in the midsize fleet.

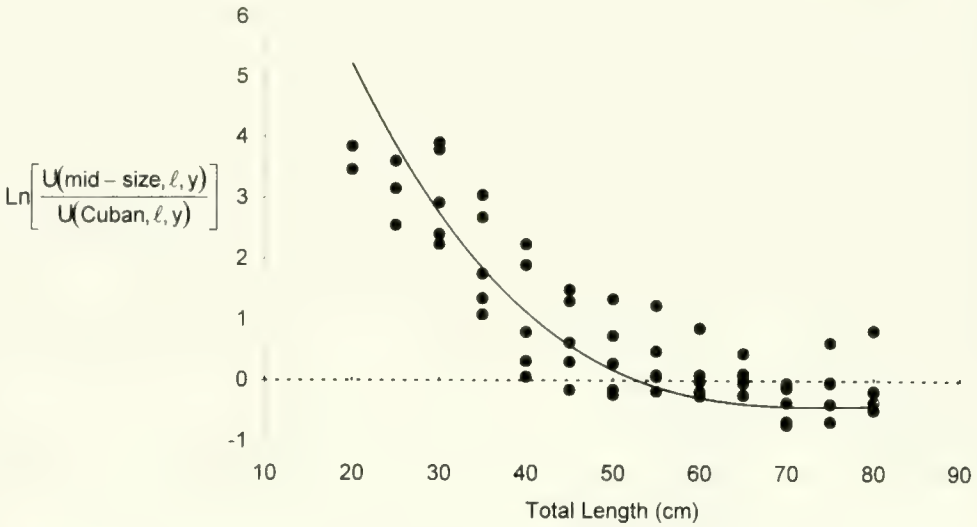

Figure 3

Trend in catchability-at-length differences, between Mexican midsize and Cuban fleets for the period 1975 to 1979, as expressed by Equation 11. Positive values indicate higher vulnerability for immature fish for the midsize fleet than for the Cuban fleet. Vulnerability of adult fish to both fleets is equal.

Table 3

Parameters of Equation 7 for the Mexican midsize and Cuban fleets for the red grouper fishery. $\alpha(y)$ expresses relative vulnerability of recruits each year and $\beta(y)$ departure of catchability trend with length, both with respect to equilibrium. (*P<0.05; **P<0.01).

Year	$\alpha(y)$ midsize	$\beta(y)$ midsize	R^2	$\alpha(y)$ Cuban	$\beta(y)$ Cuban	R^2
1973	–0.509	0.010	0.405*			
1974	0.508	–0.013	0.664*			
1975	0.511	–0.010	0.487**	–1.494	–0.018	0.602*
1976	0.953	–0.025	0.610**	0.865	–0.006	0.507**
1977	0.683	–0.022	0.600**	0.767	0.024	0.624*
1978	1.045	–0.024	0.686**	0.416	0.047	0.496*
1979	0.941	–0.021	0.757*	–1.396	0.033	0.771**
1980	–0.612	0.015	0.614**	–2.925	–0.043	0.544**
1981	0.476	–0.013	0.643**	–2.147	–0.026	0.622*
1982	0.487	–0.012	0.396*	1.923	–0.021	0.483**
1983	–0.401	0.009	0.371*	1.448	0.020	0.701**
1984	0.175	–0.005	0.446**	0.828	0.079	0.513**
1985	0.135	–0.004	0.432*	–1.126	0.026	0.661**
1986	–1.064	0.023	0.739*	–4.889	0.079	0.596**
1987	–0.915	0.013	0.581*	–1.250	0.026	0.470**

Amount of fishing and density-dependent catchability

As in Equation 9, values of $\beta(y)$ from Table 3 were fitted against fishing effort at time t. Figure 4 shows the tendency for both the midsize and Cuban fleets. For the midsize fleet, the model gives the following values for the parameters: $\alpha(E) = 0.1252$, $\beta(E) = 4.8 \cdot 10^{-6}$; $R^2 = 0.74$. Although the tendency for the Cuban fleet was also negative, the observed variability was

higher, and at least two probable tendencies were empirically identified (Fig. 4B), both of them as a consequence of changes in the catch quota assigned to the Cuban fleet. For further computations, the density-dependent effect was assumed to be similar for both fleets because of the absence of more detailed information to support quantitative analysis. This assumption is reasonable because both fleets average more than 60% overlap in a year, but almost 100% during reproductive aggregation.

Because of the evident differences in behavior between juvenile and reproductive fish, the density-dependent effect of the amount of fishing was also applied within each length class, as in Equation 9. Parameters of the model are given in Table 6. Variation of the slope $\beta(E)$ with length class is shown in Figure 5. Once again, immature fish behaved differently from adults. The density-dependent effects for immature fish were constant, whereas the same effect increased with size for sizes >50 cm TL. It is clear that the density-dependent effect during aggregation promotes a greater catchability, and because the older adult fish tend to remain longer in deeper waters (Shapiro, 1987), the density-dependent effect will increase with size (age).

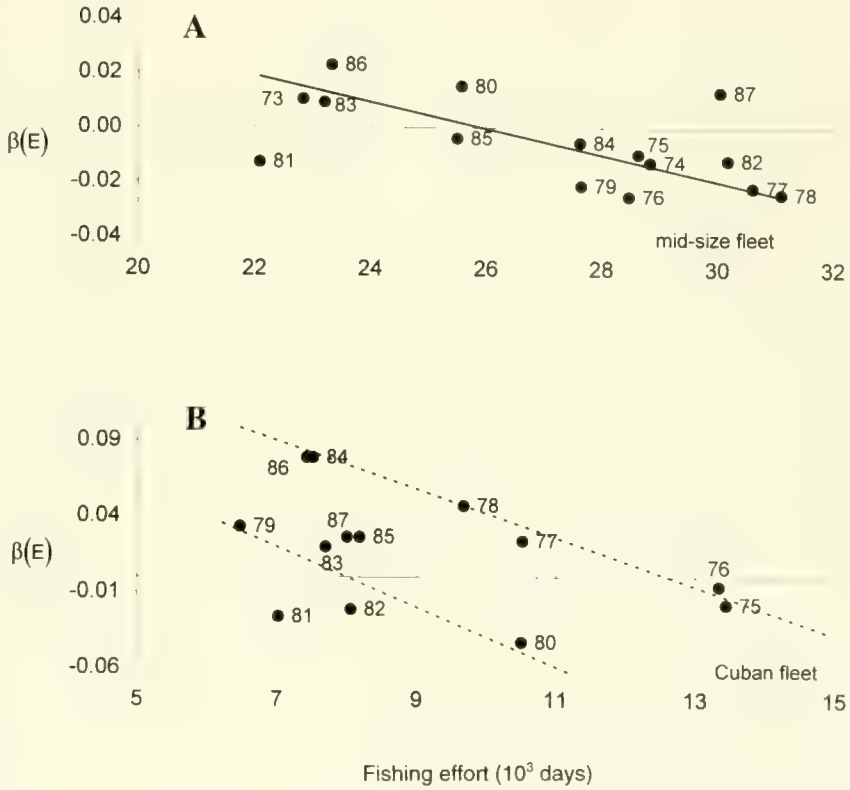

Figure 4

Estimation of density-dependent effects on catchability-at-length pattern for (**A**) the Mexican midsize fleet and (**B**) Cuban fleet of the red grouper fishery (Eq. 11). General trends suggest density-dependent effects by fleets are of the same magnitude (see text for interpretation).

The additive catchability model for the red grouper fishery

Once several sources of variation were estimated, a model (Eq. 12) was obtained by adding partial effects to the slope of Equation 13, as follows:

$$q(l,t,f,E) = \frac{0.00004256}{1+e^{-\{3.896+\beta(l,[y,m],f,E)l\}}},$$

where

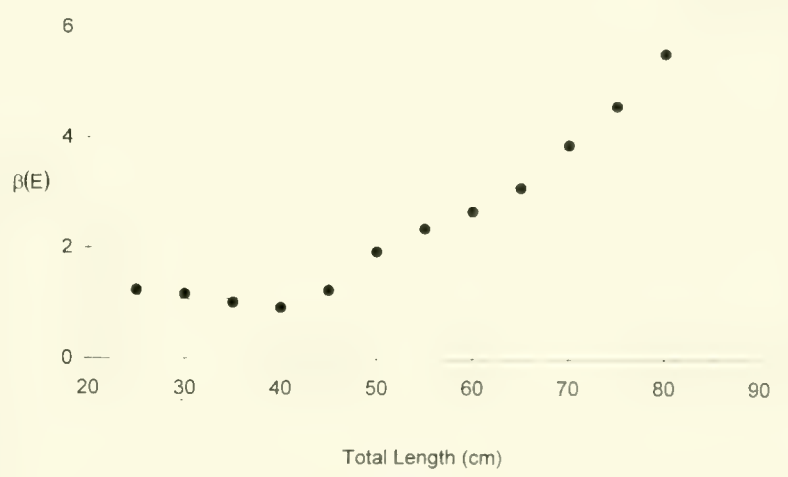

Figure 5

Trend in density-dependent effects on q within each length class with size.

Table 4

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the Cuban fleet with respect to the Mexican midsize fleet for the red grouper fishery (*P<0.05; **P<0.01).

Year	$\alpha(f)$	$\beta(f)$	R^2	n
1975	–4.474	0.052	0.636**	14
1976	–2.956	0.047	0.613*	13
1977	–3.590	0.058	0.807**	14
1978	–3.904	0.065	0.822*	12
1979	–5.186	0.076	0.795*	11
1980	–4.713	0.055	0.736*	12
1981	–6.476	0.097	0.708*	13
1982	0.323	–0.020	0.711**	9
1983	–4.527	0.051	0.713*	10
1984	–3.936	0.059	0.561**	11
1985	–3.847	0.050	0.848**	13
1986	–6.149	0.070	0.873*	13
1987	–3.942	0.055	0.606*	11

$$\beta(\ell, y, m, f, E) = \beta(\ell, \bullet) + [\beta(y), \beta(m)] + \beta(f) + \beta(E),$$

where i indexes fleet, and each constant takes the corresponding value, depending on the specific length class (ℓ), time, year (y) or month (m), fleet (f), and the specific density-dependent effect (E).

Discussion

The catchability model incorporates several sources of variation, such as individual size, time variations, and density-dependent effects, for which we assumed fishing effort is the most important variable affecting fish density, and the participation of several fishing fleets which differ in gear, catching power, and effort allocation.

The additive-catchability model, as applied to the red grouper, performed well and allows us to identify some aspects of fish behavior that influence catchability. For example, reproductive aggregation increases vulnerability of fish. Of particular importance are the relative constancy of catchability and its variance for immature individuals, and the increasing vulnerability of adult fish with size, especially during reproductive aggregation. This is related to the reproductive behavior of the population. Young fish remain close to the coast, with east–west seasonal displacements, whereas adults move across the continental shelf and aggregate during winter for reproduction. This means that juveniles and

Table 5

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the midsize fleet with respect to the artisanal fleet, both from Mexico (*P<0.05; **P<0.01).

Month	$\alpha(f)$	$\beta(f)$	R^2	n
January	2.953	–0.071	0.576*	23
February	2.654	–0.083	0.701**	22
March	4.180	–0.107	0.719*	24
April	7.904	–0.230	0.965**	14
May	2.524	–0.064	0.769*	28
June	1.295	–0.032	0.483*	31
July	1.426	–0.041	0.720*	28
August	–1.589	0.041	0.562**	16

Table 6

Estimates of parameters for Equation 9 representing density-dependent effects within each length class (n=13, df=11; *P<0.05; **P<0.01).

Total length (cm)	$\alpha(E)$ 10^{-8}	Standard error $\alpha(E)10^{-7}$	$\beta(E)$ 10^{-8}	Standard error $\beta(E)10^{-9}$	R^2
25	3.76	1.211	1.238	1.282	0.89**
30	31.05	3.356	1.164	3.471	0.50**
35	54.72	3.276	1.013	2.905	0.52**
40	48.32	1.574	0.926	2.013	0.66*
45	26.39	1.147	1.237	2.718	0.65*
50	3.68	1.091	1.936	2.426	0.85*
55	–0.31	1.123	2.360	2.974	0.85*
60	0.62	1.144	2.678	2.857	0.89*
65	1.56	1.316	3.198	1.892	0.96**
70	–1.17	1.388	3.886	2.593	0.95**
75	–2.83	1.510	4.589	2.621	0.96**
80	0.43	0.743	5.549	3.282	0.96*

adults respond differently to fleets. The model also identified the differential accessibility of specific size ranges to different fleets. This is important because, in a fully exploited fish resource such as the red grouper, controls on fishing mortality must enhance survival of spawners and recruits. Figure 6 summarizes the relation between fishing effort, maturity, and seasonal changes in catchability for the red grouper fishery. During reproductive aggregation, identified by the maturity index, vulnerability increases and vessels spend less fishing effort to obtain a given level of yields. After reproduction, groupers disperse along the continental shelf and fleets must increase fish-

ing intensity because vulnerability of fish will decrease.

For the density-dependent catchability, the model describes fish behavior reasonably well. The red grouper is a gregarious and territorial fish. Stock density is reflected straightforwardly in yields. If fish densities decrease, q will decrease, and vice versa. This response to the amount of fishing is reflected by the model.

For the catchability model, note that although a transition matrix is very helpful for the estimation process, the form of the catchability-at-length function must be interpreted with good understanding of the biology of the exploited fish resource and of the fishery. Fish biology probably is the most important aspect because the effect of other sources of variation are added to the slope of this function.

The resulting catchability model can be easily incorporated into estimations of fishing mortality and population size; i.e. for the midsize fleet at time t, fishing mortality can be expressed by

$$F(f,t,\text{midsize},E) = q(f,t,\text{midsize},E)\cdot E(t,\text{midsize}). \quad (14)$$

For the population size, the participation of the three fleets can be incorporated,

$$N\left(f,t,\sum_{f=1}^{3} f_f,E\right) = \frac{F\left(f,t,\sum_{f=1}^{3} f_f,E\right)C\left(f,t,\sum_{f=1}^{3} f_f\right)}{F\left(f,t,\sum_{f=1}^{3} f_f,E\right)\left[1-e^{-M-F\left(f,t,\sum_{f=1}^{3} f_f,E\right)}\right]}. \quad (15)$$

Despite the potential use of the catchability coefficient in some stock assessment models (i.e. age-based virtual population analysis, VPA, Pope, 1972; and length-based VPA, Jones 1981, 1984; Gulland[3]), Equations 14 and 15 suggest an alternative stock assessment tool, based on length-composition data.

A detailed description of catchability through the additive model reflecting fish behavior and fishery practices could be very useful for management purposes when it is incorporated into assessment models such as the above. Currently the red grouper fishery is subjected to heavy fishing where the main problems are intensive fishing of juveniles and the high vulnerability of adults. Because the additive catchability model describes these processes and incorporates all fleets, results can strongly aid management decisions based on a differential control of fishing mortality within the stock structure and between fleets.

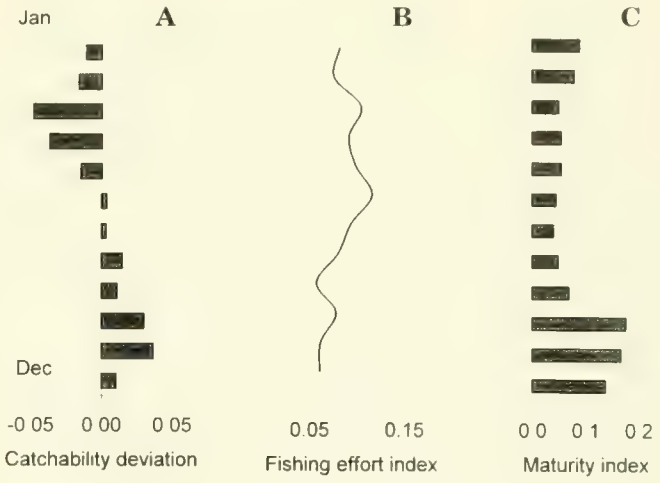

Figure 6

Schematic representation of the main q features of the red grouper fishery on the Campeche Bank: (**A**) seasonal catchability variation represented as departure of the annual average; (**B**) fishing effort index, represented as a monthly proportion of the year; (**C**) maturity index, reflecting diameter of oocytes.

Even when the model can describe the study well, we observed some critical aspects during application. The first is that we must know red grouper behavior sufficiently well to decide the form of the catchability-at-length relation (Eq. 4). Statistical criteria (i.e. a correlation coefficient) are not sufficient. A wrong interpretation of this could mean a disaster for the fishery. A second and similar aspect can occur for density-dependent catchability. The third aspect is the significance of sources of variation. Because the catchability model is based on the addition of the slopes of each particular variable and relation (i.e. with length, time, etc.), we must test that these slopes are significantly different from zero (see Equations 4, 7, 9, and 11), and if they are not different, the source of variation tested does not help to explain changes in q.

The fourth aspect involves the number of parameters to be estimated, which usually is taken as proportional to the complexity of the model computations, and inversely related to applicability. For the present case, the number of parameters in the model is $n + 2$, where n is the number of sources of varia-

[3] Gulland, J. A. 1965. Estimation of mortality rates. Annex to rep. Arctic Fish. Working Group. ICES Council Meeting (CM), 1965, paper 3, 9 p.

tion to be considered. However, the number of constants to be estimated strongly increases with the length of the time-series of data as $3(m \bullet y \bullet f) + 2(\ell) + 2$, with m = number of months, y = number of years, f = number of fleets, and ℓ = number of length classes. For example, in our study case, with $y = 13$, $f = 2$, and $\ell = 12$, the number of constants to be estimated will be 104. We think these are a lot of parameters; however, they are easily estimated because all of them are obtained by regression or by an analogous technique.

Acknowledgments

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Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf*

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Abstract.—After spending summer months in estuaries, spring- and summer-spawned young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, migrate out to continental shelf waters of the Mid-Atlantic Bight in early autumn. Adult bluefish are found on the continental shelf throughout summer and fall. Both juveniles and adults have high food consumption rates and are generally piscivorous. To determine principal prey types on the shelf, dietary analyses were performed on YOY and adult bluefish collected from National Marine Fisheries Service autumn bottom trawl surveys in 1994 and 1995. Both spring- and summer-spawned YOY bluefish diets were dominated by bay anchovy. However, the significantly larger size of the spring-spawned cohort was associated with the consumption of other prey species such as squid, butterfish, striped anchovy, and round herring. Summer-spawned bluefish were significantly smaller in 1995 than in 1994; diet and prey size comparisons suggest that body size had a dramatic influence on the amount of piscivorous feeding in the summer-spawned cohort. Adult bluefish diet was dominated by schooling species such as squid, butterfish, and clupeids. Cannibalism was virtually nonexistent. Daily ration estimates of YOY bluefish on the shelf (4–12% body wt/d) were similar to estuarine estimates in late summer. It is estimated that during the month of September, YOY bluefish in aggregate consumed 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995. The effect of this predatory loss on population dynamics of bay anchovy and the fish community on the continental shelf is unknown.

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One of the dominant marine piscivores along the U.S. east coast is the bluefish, *Pomatomus saltatrix* (Juanes et al., 1996). Bluefish spawned in offshore waters of the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move into mid-Atlantic Bight estuaries in June at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits consisting of summer-spawned fish occur in nearshore waters from mid to late summer.

In estuaries, bluefish exhibit rapid growth rates that are fueled by high food consumption and evacuation rates (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1996). In the Hudson River estuary, for example, predation by bluefish is high enough to account for virtually all natural mortality of young-of-the-year (YOY) striped bass during their summer–fall growing season (Buckel et al., 1999). After spending the summer months in estuaries, YOY bluefish migrate back out onto the shelf and migrate southward to overwinter (Munch and Conover, in press). Spring-spawned YOY bluefish migrate out of estuaries at a size of ~180 mm fork length (FL) and ~100 g (Nyman and Conover, 1988; McBride and Conover 1991). By age 1, these spring-spawned fish attain sizes of ~260 mm FL and weights of ~300 g (Chiarella and Conover, 1990). Therefore, an individual spring-spawned bluefish gains from 100 to 200 g during its autumn migration. Given a 15% gross growth efficiency (Juanes and Conover, 1994; Buckel et al. 1995), a single bluefish could thus consume from ~650 to 1300 g of prey.

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Compared with the nearshore phase of the early life history of bluefish, our knowledge of the foraging ecology and predatory impact of bluefish on the continental shelf is poor. Here we quantify the diet of YOY and adult bluefish and determine YOY bluefish prey type and size selectivity patterns, foraging chronology, daily ration, and biomass of prey consumed during the autumn migration on the shelf.

Methods

Study area and collections

YOY and adult bluefish and their potential prey were collected on the U.S. east coast continental shelf during the autumn of 1994 and 1995 aboard the research vessel *Albatross IV*. Collections were made during the National Marine Fisheries Service, Northeast Fisheries Science Center's (NMFS-NEFSC) autumn bottom trawl survey cruises at predetermined stations from Cape Hatteras, NC, to Nova Scotia. Cruises began in early September and ended in late October in both years (6 September to 28 October 1994 and 5 September to 27 October 1995).

Descriptions of the survey design and the trawl characteristics can be found in Azarovitz (1981). Briefly, tows were made with a no. 36 Yankee trawl equipped with rollers with an opening 3.2 m high, 10.4 m wide, with 12.7-cm stretched mesh in the opening, with 11.4-cm stretched mesh in the codend, and with a 1.25-cm stretched mesh lining in the codend and upper belly to retain YOY fishes. Tows were 30 minutes in duration at 3.5 knots in relation to bottom and were conducted on a 24-h basis.

Dietary analyses

Adult and YOY bluefish were distinguished by using length-age relationships. Munch and Conover (in press) examined the annual size distributions of bluefish from autumn bottom trawl surveys conducted since the 1970s in four different regions of the shelf: SOC=South of Chesapeake Bay; C–D=Chesapeake Bay to Delaware Bay; SNE=Southern New England (Delaware Bay to Narragansett Bay); and Georges Bank. On the basis of these size distributions and backcalculated sizes at age 1 (Chiarella and Conover, 1990, and references therein), they classified YOY bluefish in autumn as those fish ≤300 mm FL. We classified adults as those bluefish >300 mm FL and we distinguished spring- and summer-spawned YOY bluefish for each region in 1994 and 1995 on the basis of bimodality in length-frequency distributions (Munch and Conover, in press). We also adopted Munch and Conover's (in press) geographical boundaries for this analysis. In 1994, summer-spawned bluefish sizes by region were as follows: SOC, FL≤120 mm; C–D, FL≤160 mm; and SNE, FL≤160 mm. In 1995, summer-spawned bluefish sizes were as follows: SOC, FL≤100 mm; C–D, FL≤150 mm; and SNE, FL≤140 mm. Spring-spawned bluefish were those fish larger than the summer-spawned cohort by region but ≤300 mm FL.

Diets of spring- and summer-spawned juveniles and adult bluefish were quantified. Bluefish taken for stomach content analysis were wet weighed (±1.0 g) and measured for fork length, FL (to 1.0 mm). Stomachs were removed at sea and preserved in 10% formalin buffered with sea water. On some occasions, whole fish were either frozen or preserved in 10% formalin and then processed in the laboratory. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (±0.01 g), and measured (TL for fish prey and mantle length for squid, ±1.0 mm). Eye diameter (±0.1 mm) and caudal peduncle height (±0.1 mm) were measured for partially eaten bay anchovy and butterfish prey and converted into TL from linear regression equations (Scharf et al., 1997; Scharf et al., 1998a).

Each trawl containing bluefish provided us with a group or "cluster" of bluefish for a given station. Therefore, for our analysis, the mean and variance of diet indices were calculated with cluster sampling estimators developed at the NEFSC-NMFS, Woods Hole, MA (Cochran, 1977, Fogarty, unpubl. data). These calculations are described in a previous study that examined bluefish diet in the Hudson River estuary (Buckel et al., 1999).

Net feeding

During a 30-minute tow, bluefish may feed within the trawl (an activity known as net feeding). Net feeding could bias the diet index estimates or affect gut fullness level estimates (or do both). We tested for such bias by classifying fish or squid prey as either 1) "fresh" or 2) "digested" during our stomach content examination. "Fresh" prey had no sign of digestion and "digested" prey were either partially or well digested (e.g. they were anywhere from starting to lose skin to being only identifiable by skeleton or shape). The percent occurrence of four dominant prey (bay anchovy, striped anchovy, butterfish, and squid) were compared between fresh and digested categories in YOY bluefish. If the percent occurrence of each prey category within a cohort and region was similar for fresh and digested prey, it would suggest that either there was no net feeding or that it did not affect diet index estimates.

Prey-type selectivity

The feeding selectivity of spring-spawned bluefish on the continental shelf was determined from the relative abundance of prey in individual bluefish guts and the relative abundance of prey in trawl catches. Four prey categories were examined in 1994 (bay anchovy, butterfish, squid, and "other") and three prey categories in 1995 (bay anchovy, squid, and "other"). The "other" category included any teleost fish that did not fall into the previously mentioned groups. The relative abundance of these prey in the field was calculated by including only those prey that were of a size that bluefish could theoretically consume (prey FL<80% of bluefish FL; determined from an independent study, Scharf et al., 1997). Additionally, the index was calculated for stations where at least ten spring-spawned bluefish were captured. Chesson's (1978) index was used to determine bluefish prey preference as

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^{m} r_j / p_j}, \qquad i = 1,\ldots\ldots,m,$$

where α_i = the selectivity for prey type i for an individual bluefish;
r_i = the relative abundance of prey type i in an individual bluefish stomach;
p_i = the relative abundance of prey type i in the environment; and
m = the number of prey types available.

Values of α_i were averaged for each year. Random feeding occurs when mean $\alpha_i = 1/m$ (1994=0.25 and 1995=0.33); values of $\alpha_i > 1/m$ or $\alpha_i < 1/m$ represent "selection" and "avoidance" of prey, respectively. Random feeding was tested by using a t-test to compare mean α_i with $1/m$ for each prey type within each year (Chesson, 1983).

Prey-size relationships and size selectivities

Prey sizes of all bluefish prey were measured directly or determined indirectly from regression equations. The relationship between ingested prey size and bluefish length was determined for YOY and adult bluefish in both 1994 and 1995. In order to compare the relative prey size ingested by spring- and summer-spawned bluefish cohorts in 1994 and 1995, the frequency distributions of bay anchovy FL to bluefish FL ratios were examined. Ratios were calculated for all bay anchovy prey that were measured (1994, n=388; 1995, n=202).

Size-selective feeding on bay anchovy prey was examined by comparing the sizes of bay anchovy ingested by bluefish at a specific station with sizes of bay anchovy captured in the trawl at that station. Stations from 1994 and 1995 that had n>15 bay anchovy length measurements for each bluefish cohort were used in the analysis. Bay anchovy lengths at each station were obtained from archived data at NEFSC-NMFS, Woods Hole, MA.

Selectivity for bay anchovy prey size categories was measured by using Chesson's (1978) index (described above). Bay anchovy lengths ingested by bluefish and collected at each station were partitioned into four bay anchovy FL categories: 25–34, 35–44, 45–54, and 55–64 mm. Values of α_i were calculated from individual bluefish for each size bin at each station separately; these were then averaged across stations. As above, values of $\alpha_i > 1/m$ or $\alpha_i < 1/m$ represent "selection" and "avoidance" of size categories, respectively. Estimated values of mean α_i were compared with $1/m$ by using a t-test (1994 spring-spawned, $1/m$=0.25, and summer-spawned, $1/m$=0.33; 1995 spring-spawned, $1/m$=0.33).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Values of gut fullness were used to examine feeding chronology of YOY bluefish. Gut fullness values (F) were calculated as

$$F = G/W,$$

where G = prey wet weight; and
W = bluefish wet weight (total weight minus prey wet weight).

Gut fullness values for individual bluefish were pooled over eight 3-h time periods and averaged. This analysis was performed for both spring- and summer-spawned bluefish by geographic region.

In order to estimate feeding rates of bluefish on the shelf, bluefish gastric evacuation rate (GER) estimates were needed. Previous work on YOY bluefish GER showed that prey type and bluefish body size did not have a significant effect on bluefish GER; of the factors examined, temperature had the only significant effect on bluefish GER (Buckel and Conover, 1996). These laboratory experiments described bluefish GER from 21° to 30°C. In our continental shelf collections, YOY bluefish were found in water temperatures as low as 15°C (mean of surface and bottom temperature). Therefore, a laboratory experiment to measure YOY bluefish GER at 15°C was performed.

The experiment was conducted in an identical manner to previous GER experiments on YOY blue-

fish (Buckel and Conover, 1996). Briefly, YOY bluefish were acclimated to experimental tanks for two weeks, acclimated to 15°C for 3 days, and then held at 15°C for a 12–48 h starvation period. They were then fed a single meal of previously frozen and thawed adult bay anchovy (bluefish sizes were: mean bluefish TL=122 [range=99–146], mean wet weight=15.79 g, prey mean wet weight=0.88 g, mean prey wt/predator wt=5.8%). After a predetermined period of time, individual bluefish were sacrificed and their stomach contents removed, blotted dry, and weighed (±0.01 g).

The exponential GER model (see Buckel and Conover, 1996) was fitted to the proportion of meal remaining versus time by using nonlinear regression analysis. The GER estimate from this experiment was used along with estimates from Buckel and Conover (1996) to develop an empirical function describing YOY bluefish GER from 15° to 30°C. This function was used to estimate bluefish GER from water temperatures at which bluefish were collected on the continental shelf. Bluefish daily ration was estimated for each cohort by region in 1994 and 1995 with the Eggers (1979) equation:

$$D = \bar{F}_i \cdot R_e \cdot 24,$$

where D = is bluefish daily ration;
$\bar{F}_i$ = the mean gut fullness over 24 hour; and
R_e = the exponential gastric evacuation rate (see above).

Mean gut fullness was calculated by taking the average of the individual time period (i) gut fullness means from the feeding chronology analysis (see above). The mean of the means was used to give each time period equal weight even though sample sizes for given time intervals varied over the diel cycle. Daily ration was calculated for those geographical regions and cohorts that had a sufficient diel record (e.g. gut fullness estimates throughout the diel cycle). The standard error of the daily ration estimate was approximated by using the delta method (Seber, 1973).

Estimates of the biomass of prey consumed by the YOY bluefish population during their southward migration requires estimates of the numbers of YOY bluefish in the population. The NEFSC, NMFS, Woods Hole, MA, has used virtual population analysis (VPA) to estimate the abundance of the east coast bluefish population (NEFSC[1]). These estimates of YOY bluefish abundance in 1994 and 1995 were used to calculate the daily consumption of bay anchovy by the YOY bluefish population in the following steps. First, the biomass of the spring- and summer-spawned cohorts on the shelf was calculated. This was done by determining the numbers in each spawning cohort (this was necessary because the VPA was for all YOY combined) based on relative abundance estimated from the NMFS autumn bottom trawl survey and then multiplying by the average individual fish weight in each cohort. Secondly, this cohort biomass was multiplied by the estimates of daily ration (lowest and highest) to determine the daily biomass of prey consumed by each cohort. To determine the amount of bay anchovy consumed daily, each cohort's biomass was multiplied by the mean proportion of bay anchovy by weight in each cohort's diet. Finally, a daily estimate of the numbers of bay anchovy consumed by the YOY bluefish population was calculated by dividing the biomass of bay anchovy consumed by the average bay anchovy weight ingested by each cohort. Bay anchovy weight was calculated from mean bay anchovy length ingested with regressions from Hartman and Brandt (1995a).

Results

Dietary analyses

The stomach contents of 989 young-of-the-year (626 spring- and 363 summer-spawned) and 275 adult bluefish were examined. All YOY bluefish were captured between 12 and 29 September 1994 and 7 and 23 September 1995. Continental shelf bluefish diets were dominated by teleost fish and squid prey (see Table 1 for common and scientific names of bluefish prey).

In both 1994 and 1995, the dominant fish prey of spring-spawned bluefish in all three geographical regions was bay anchovy (Table 2). Other spring-spawned bluefish prey included long-finned squid, striped anchovy, butterfish, and round herring. Butterfish were slightly more important in 1994 than in 1995. Also in 1994, amphipods made up a substantial portion of spring-spawned bluefish diets in the SNE region. In 1995, channeled whelk were a relatively important prey of bluefish in the C–D region; the foot and operculum were found in bluefish collected over a large geographical area.

The dominant fish prey of summer-spawned bluefish across all geographical regions was bay anchovy in both 1994 and 1995 (Table 3). The incidence of long-finned squid in summer-spawned bluefish diets was low; however, other invertebrates such as

[1] NEFSC. 1997. Report of the 23rd Northeast Regional Stock Assessment Workshop (23rd SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. Northeast Fisheries Sci. Cent. Ref. Doc. 97-05, 191 p. [Available from National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.]

amphipods, mysids, crab larvae, and copepods were relatively important prey. This was particularly true for the relatively small size summer-spawned bluefish collected in the SNE in 1995; the diet of these fish were dominated by copepods (Table 3).

The diet of adult bluefish collected in the Georges Bank region was dominated by butterfish, squid, round herring, and Atlantic herring in both 1994 and 1995 (Table 4). There were several commercially important species consumed by adult bluefish on Georges Bank in 1994. These included American plaice, haddock, Atlantic cod, and several hake species. A large component of the diet of adult bluefish from Cape Hatteras to Montauk Point, NY, was bay anchovy. Butterfish, round herring, and squid were also important prey of bluefish collected from this geographical region. The diet of bluefish from both regions also included several other fish and invertebrate species (Table 4). Channeled whelk were preyed upon by adult bluefish in the same region and year that spring-spawned YOY bluefish were found to feed on them.

Table 1

Common and scientific names of bluefish prey items on the continental shelf and Georges Bank.

Common name	Scientific name
Fish	
American plaice	*Hippoglossoides plattessoides*
Atlantic cod	*Gadus morhua*
Atlantic herring	*Clupea harengus*
Atlantic mackerel	*Scomber scombrus*
Atlantic silverside	*Menidia menidia*
bay anchovy	*Anchoa mitchilli*
butterfish	*Peprilus triacanthus*
conger eel	*Conger oceanicus*
fawn cusk eel	*Lepophidium cervinum*
fourbeard rockling	*Enchelyopus cimbrius*
haddock	*Melanogrammus aeglefinus*
Northern pipefish	*Syngnathus fuscus*
Northern puffer	*Sphoeroides maculatus*
ocean pout	*Macrozoarces americanus*
planehead filefish	*Monacanthus hispidus*
red hake	*Urophycis chuss*
round herring	*Etrumeus teres*
sand lance	*Ammodytes* spp.
scup	*Stenotomus chrysops*
sea horse	*Hippocampus erectus*
searobin	*Prionotus* spp.
silver hake	*Merluccius bilinearis*
margined snake eel	*Ophicthus cruentifer*
spot	*Leiostomus xanthurus*
striped anchovy	*Anchoa hepsetus*
weakfish	*Cynoscion regalis*
white hake	*Urophycis tenuis*
windowpane	*Scophthalmus aquosus*
Invertebrates	
amphipods	*Gammarus* spp.
boreal squid	*Illex illecebrosus*
blue crab	*Callinectes sapidus*
cancer crab	*Cancer* spp.
channeled whelk	*Busycon canaliculatum*
fiddler crab	*Uca* spp.
lady crab	*Ovalipes ocellatus*
long-finned squid	*Loligo pealei*
mole crab	*Emerita talpoida*
sand shrimp	*Crangon* spp.

Net feeding

Although there was evidence of net feeding, it did not seem to bias diet indices. The percent occurrence of several different prey found to be "fresh" and the percent occurrence of these same prey found to be "digested" was similar (Table 5). Only in spring-spawned bluefish in the SNE region in 1995 were there more fresh prey than digested prey in their diet (30 fresh vs. 19 digested; Table 5). Spring-spawned bluefish had more freshly eaten prey in their diet (20–61%) than summer-spawned bluefish (0–26%).

Prey-type selectivity

Spring-spawned YOY bluefish selected positively ($\alpha > 1/m$) for bay anchovy in both 1994 (α=0.69, t-test vs. 0.25, t=8.05, df=154, P<0.001)) and 1995 (α=0.80, t-test vs. 0.33, t=6.40, df=74, P<0.001). However, YOY bluefish avoided ($\alpha < 1/m$) butterfish, squid, and "other" (determined for 1994 only) prey fish in 1994 (t-tests vs. 0.25; P<0.001) and 1995 (t-tests vs. 0.33, P<0.05) (Table 6).

Prey-size relationships and selectivities

There was a very weak but significant positive linear relationship between fish prey TL and YOY bluefish FL in 1994 (r^2=0.10, P<0.0001, n=418) and 1995 (r^2=0.02, P=0.027, n=224) (Fig. 1). A positive linear relationship also existed for fish prey TL and adult bluefish FL in 1994 (r^2=0.15, P<0.001, n=90) and 1995 (r^2=0.28, P<0.0001, n=100) (Fig. 2). Although there was a significant increase in mean prey sizes taken, juvenile and adult bluefish continued to take small prey with increasing body size.

Bay anchovy to bluefish FL ratios were higher in the summer-spawned bluefish cohort than in the spring-spawned cohort in 1994 and 1995. Additionally,

Table 2

Stomach contents of spring-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %W=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish												
bay anchovy	71.4 (32.9)	45.7 (21.9)	35.7 (22.9)	40.4 (23.6)	25.0 (54.1)	6.0 (28.0)	57.2 (62.9)	83.2 (59.2)	50.2 (9.0)	50.1 (14.4)	47.4 (38.1)	43.8 (39.3)
butterfish	5.5 (3.4)	8.9 (6.0)	14.7 (7.5)	38.9 (19.0)	12.5 (97.5)	48.1 (375.2)	1.7 (8.8)	1.6 (9.4)			1.9 (4.5)	3.5 (8.2)
round herring	4.4 (2.4)	10.3 (7.6)					4.3 (3.1)	0.8 (5.7)	0.6 (0.9)	3.3 (5.5)		
striped anchovy	1.4 (3.1)	1.8 (4.2)	3.9 (4.9)	10.0 (10.8)	12.5 (123.9)	33.4 (331.1)	3.0 (16.8)	5.8 (29.3)	5.1 (3.3)	8.5 (5.7)	3.8 (6.3)	2.6 (4.6)
bluefish									1.1 (1.4)	2.9 (4.1)	1.9 (4.4)	4.2 (9.8)
silver hake	2.3 (6.0)	2.9 (7.6)										
seahorse									0.6 (0.9)	0.2 (0.3)		
margined snake eel											1.9 (4.4)	7.1 (16.2)
Serranidae											3.8 (5.9)	4.6 (8.9)
Sparidae											1.9 (4.2)	6.2 (13.6)
Clupeidae							0.4 (3.1)	1.8 (12.6)	0.6 (0.9)	2.8 (4.7)		
Unidentified fish	16.0 (10.8)		11.6 (5.6)		12.5 (97.5)		7.0 (27.2)		16.6 (5.6)		14.1 (9.3)	
Invertebrates												
long-finned squid	10.5 (7.4)	14.8 (16.0)	1.6 (2.0)	1.1 (1.7)			5.7 (25.6)	3.2 (13.0)	1.7 (1.6)	7.9 (9.6)	1.9 (9.3)	4.2 (7.2)
crab[1]	2.0 (3.9)	4.0 (10.6)									3.8 (6.6)	0.6 (1.0)
amphipods	31.2 (20.2)	11.1 (10.4)					3.0 (14.1)	1.9 (9.2)				
unidentified shrimp												
crustacean larvae[2]			1.6 (2.2)	0.9 (1.7)					2.2 (1.7)	0.6 (1.0)		
polychaete	1.4 (3.0)	<0.1 (0.3)	0.8 (1.4)	0.3 (0.5)								
channeled whelk									9.0 (8.1)	11.6 (9.3)		
Total stomachs analyzed	182		129		8		79		177		51	
Number containing prey	157		81		5		57		140		39	
Mean FL (mm, SE)	208 (2)		243 (4)		263 (14)		212 (2)		244 (3)		261 (3)	
FL range (mm)	161–270		161–300		200–300		180–300		160–300		200–300	
Mean wt (g, SE)	124.9 (3.5)		219.2 (9.4)		247.4 (33.8)		129.7 (5.0)		203.6 (7.3)		247.5 (9.3)	
Wt range (g)	51–256		49–398		116–343		75–342		50–371		105–365	

[1] Lady crab, mole crab, unidentified crab
[2] Lady crab, *Penaeus* spp., unidentified crustacean larvae

Table 3

Stomach contents of summer-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish												
bay anchovy	80.1 (30.1)	90.9 (7.1)	33.7 (72.5)	71.7 (70.0)	16.7 (250.0)	50.0 (750.0)	23.6 (113.5)	34.3 (145.7)	45.1 (32.3)	86.6 (33.5)	23.5 (72.6)	76.5 (253.4)
Atlantic silverside	0.3 (1.2)	0.9 (3.7)										
searobin larvae			8.1 (60.8)	0.8 (3.1)								
Unidentified fish	15.3 (9.9)		14.8 (23.1)		33.3 (0.0)		27.9 (33.1)		50.4 (32.5)		41.2 (63.6)	
Invertebrates												
long-finned squid	0.6 (2.1)	<0.1	3.6 (33.7)	1.4 (6.6)			1.7 (10.4)	1.7 (10.4)				
crab[1]	0.5 (2.0)	1.0 (3.7)										
crab larvae[2]	1.1 (4.0)	<0.1	12.4 (24.3)	3.7 (7.4)								
amphipods	19.1 (11.0)	7.0 (5.3)	3.9 (8.5)	0.8 (1.8)								
mysids			23.6 (139.6)	20.4 (71.2)	16.7 (250.0)	12.2 (182.4)						
copepods					16.7 (250.0)	8.7 (131.8)	44.7(149.1)	48.5 (186.0)				
sand shrimp	0.1 (0.5)	<0.1										
polychaete	<0.1	<0.1			16.7 (250.0)	29.1 (435.8)						
isopod			1.4 (10.1)	1.0 (3.6)								
Total stomachs	200		66		6		61		53		17	
Number containing prey	165		56		4		52		38		11	
Mean FL (mm, SE)	135 (1)		133 (2)		96 (12)		70 (3)		90 (3)		77 (3)	
FL range (mm)	86–160		107–160		37–120		20–140		60–150		60–100	
Mean wt (g, SE)	31.2 (0.9)		29.2 (1.4)		11.3 (2.4)		4.8 (0.6)		10.9 (1.3)		5.0 (0.6)	
Wt range (g)	6–64		10–53		1–19		0.1–32		2–45		3–12	

[1] Mole crab and unidentified crab
[2] Lady crab, blue crab and fiddler crab

Table 4

Stomach contents of adult bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994				1995			
	Georges Bank		Hatteras–Montauk		Georges Bank		Hatteras–Montauk	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish								
bay anchovy			25.9 (51.8)	21.4 (47.7)			36.4 (34.6)	34.9 (44.9)
butterfish	27.8 (28.7)	18.6 (23.6)	9.4 (18.5)	12.7 (30.0)	7.6 (38.0)	16.3 (80.2)	5.6 (12.0)	9.0 (20.8)
round herring	3.7 (9.2)	2.2 (5.6)	6.8 (17.4)	26.5 (87.9)	7.6 (41.8)	10.8 (66.4)	3.7 (9.1)	3.6 (11.1)
striped anchovy			1.8 (7.9)	1.7 (7.7)	2.2 (21.4)	5.2 (51.5)	3.9 (12.3)	5.0 (13.2)
bluefish							0.5 (2.3)	0.9 (4.7)
planehead filefish							0.5 (2.3)	0.2 (1.4)
Northern puffer							0.9 (4.6)	0.8 (4.0)
Northern pipefish	1.9 (7.5)	0.6 (2.5)						
searobin			1.8 (6.2)	2.1 (8.8)	2.2 (21.9)	6.5 (65.3)	0.5 (2.3)	1.1 (5.4)
weakfish			2.2 (7.8)	3.0 (12.9)			0.5 (2.3)	0.1 (0.6)
spot								
sand lance							0.5 (2.3)	0.9 (4.7)
scup			2.7 (7.9)	1.5 (4.5)			0.5 (2.3)	0.1 (0.5)
Atlantic herring	7.4 (17.6)	11.3 (23.7)			10.9 (54.7)	17.6 (85.0)	0.5 (2.3)	0.1 (0.7)
Atlantic mackerel			0.9 (4.2)	0.9 (4.3)				
fawn cusk eel							0.5 (2.3)	<0.1
conger eel							0.5 (2.3)	1.5 (7.2)
ocean pout			0.9 (4.3)	0.9 (4.3)	2.2 (22.9)	2.2 (22.9)	0.5 (2.3)	0.3 (1.7)
fourbead rockling	1.9 (7.5)	1.7 (7.0)						
American plaice	1.9 (7.6)	0.8 (3.5)						
windowpane	5.6 (22.0)	5.6 (22.0)			2.2 (21.9)	5.2 (51.9)		
silver hake	1.9 (7.6)	1.0 (4.2)			4.3 (39.5)	8.4 (76.3)		
white hake	1.9 (7.5)	2.4 (9.9)						
red hake	1.9 (6.7)	2.1 (7.6)					1.9 (7.4)	1.7 (6.7)
haddock	1.9 (7.5)	2.0 (8.0)			2.2 (21.9)	0.8 (8.4)		
Atlantic cod	3.7 (10.3)	6.7 (20.6)						
Gadidae	1.9 (7.6)	1.9 (7.6)						
Unidentified fish	29.6 (32.1)		26.1 (43.1)		30.4 (70.7)		21.9 (23.4)	
Invertebrates								
long-finned squid	29.6 (25.6)	23.7 (29.4)	11.6 (22.1)	5.2 (11.3)	15.2 (53.6)	18.1 (89.2)	7.7 (11.8)	10.9 (27.0)
boreal squid	11.1 (23.7)	8.4 (19.4)						
lady crab	3.7 (15.0)	1.2 (4.7)						
cancer crab	1.9 (7.2)	0.6 (2.5)						
unidentified crab			0.9 (4.1)	0.8 (3.5)	2.7 (22.9)	0.4 (3.7)	1.3 (4.6)	0.1 (0.4)
amphipods			0.9 (4.3)	0.9 (4.3)				
unidentified shrimp					4.3 (30.8)	2.0 (19.1)		
polychaete							2.0 (6.8)	4.9 (16.7)
channeled whelk							9.0 (33.2)	13.0 (41.9)
Total stomachs analyzed	50		65		44		116	
Number containing prey	45		45		32		84	
Mean FL (mm, SE)	653 (10)		451 (18)		607 (17)		391 (11)	
FL range (mm)	420–780		310–780		380–750		310–730	
Mean wt (g, SE)	3837 (151)		1546 (170)		3082 (225)		991 (106)	
Wt range (g)	1209–6151		368–5965		692–6530		319–4570	

the prey to predator FL ratios for summer-spawned bluefish were higher in 1995 than they were in 1994 (Fig. 3). Summer-spawned bluefish consumed relatively larger bay anchovies in 1995 than in 1994; this was due to both the smaller size of the summer-spawned cohort in 1995 and the larger bay anchovy prey. A linear function describing bluefish capture success as a function of prey length to bluefish length ratio from Scharf et al. (1998b) is also plotted in Figure 3 (capture success data for bluefish feeding on Atlantic silversides). The distribution of ratios for both spring- and summer-spawned bluefish in 1994 and spring-spawned bluefish in 1995 are values for which bluefish have relatively high capture success;

Table 5

The total number of prey (n) found either fresh or digested (fresh=no sign of digestion; digested=prey skinless to being only identifiable by skeleton or shape) in spring- and summer-spawned young-of-the-year bluefish stomachs and the percentage contribution of bay anchovy, striped anchovy, butterfish, and squid for these categories. Bluefish were captured during 1994 and 1995 National Marine Fisheries Service autumn bottom trawl surveys. Bluefish were collected from three geographical locations of the Mid-Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC=South of Chesapeake Bay, after Munch 1997).

		Spring-spawned		Summer-spawned	
Location	Prey type	No. fresh (%)	No. digested (%)	No. fresh (%)	No. digested (%)
1994					
SNE	n	19	51	0	31
	bay anchovy	89.5	56.9		
	striped anchovy	5.3	7.8		
	butterfish	5.3	33.3		
	squid	0	2.0		
C–D	n	46	107	36	104
	bay anchovy	89.1	76.6	100	97.1
	striped anchovy	2.2	2.8	0	0
	butterfish	2.2	7.5	0	1.0
	squid	6.5	13.1	0	2.0
1995					
SNE	n	30	19	0	57
	bay anchovy	73.3	68.4		
	striped anchovy	6.7	10.5		
	butterfish	3.3	15.8		
	squid	16.7	5.3		
C–D	n	21	82	0	36
	bay anchovy	81.0	82.8		
	striped anchovy	19.0	13.8		
	butterfish	0	0		
	squid	0	3.4		

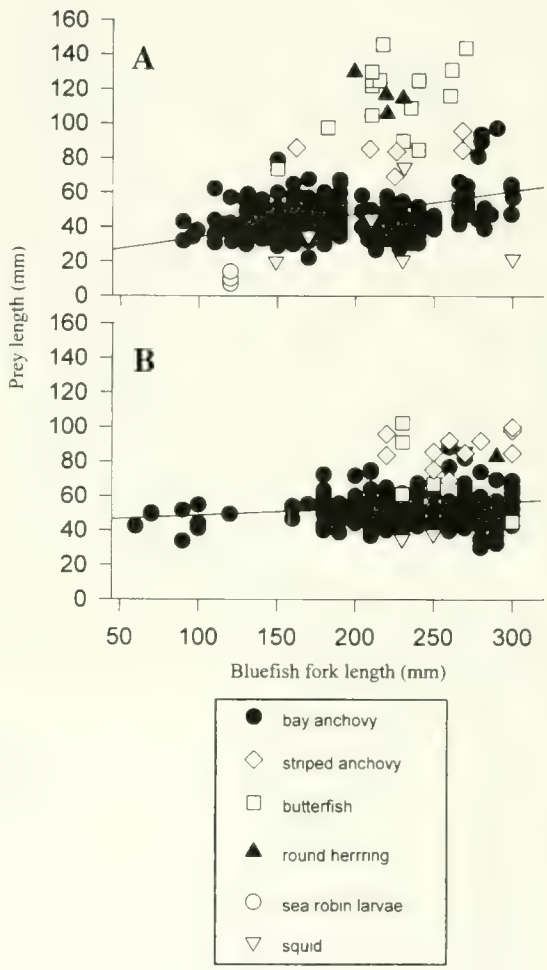

Figure 1

Prey total length (mantle length for squid) versus YOY bluefish fork length in (**A**) 1994 (*prey TL*=0.134 × *bluefish FL*+20.826, r^2=0.10, P<0.0001) and (**B**) 1995 (*prey* TL=0.041 × *bluefish FL*+44.538, r^2=0.02, P=0.027).

Table 6

Prey selectivity (Chesson's α, see text for calculations) in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of α =1/m (where "m" is the number of prey categories) represent random feeding, whereas values of α > 1/m or α < 1/m represent "selection" and "avoidance" of prey, respectively. Values significantly different from 1/m (t-test, P<0.05) are indicated by a (+) for "selection" or (–) for "avoidance".

Prey type	1994 (1/m=0.25)	1995 (1/m=0.33)
Bay anchovy	0.69 (+)	0.80 (+)
Butterfish	0.12 (–)	0.03 (–)
Squid	0.09 (–)	0.18 (–)
Other	0.11 (–)	—

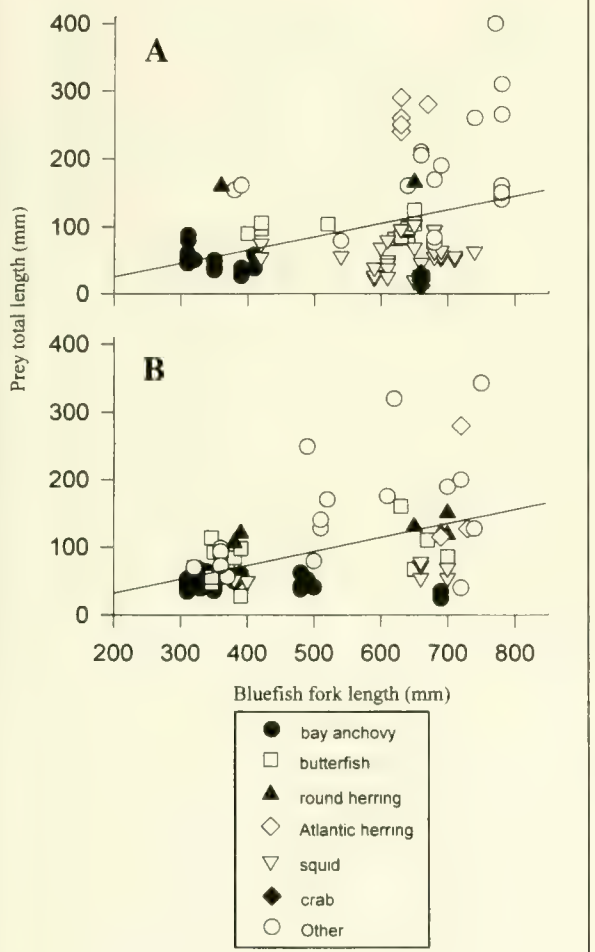

Figure 2

Prey total length (mantle length for squid) versus adult bluefish fork length in (**A**) 1994 (*prey TL*=0.199 · *bluefish FL*–14.413, r^2=0.15, P<0.001) and (**B**) 1995 (*prey TL*=0.205 × *bluefish FL*–9.047, r^2=0.28, P<0.0001). "Other" prey include searobin, red hake, silver hake, unidentified gadid, scup, windowpane, haddock, Northern puffer, conger eel, cusk eel, sand lance, striped anchovy, spot, weakfish, Atlantic mackerel, fourbeard rockling, and ocean pout.

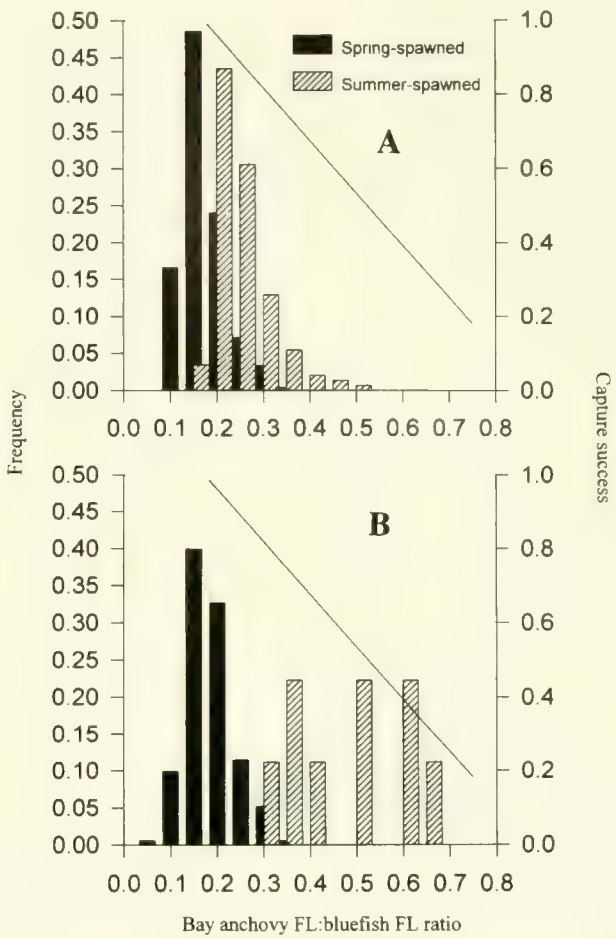

Figure 3

Bay anchovy FL to bluefish FL ratios for both spring-and summer-spawned bluefish in (**A**) 1994 and (**B**) 1995. Regression line for capture success versus prey length to predator length ratio from Scharf et al. (1998b).

however, the prey length to predator length ratios of summer-spawned bluefish in 1995 are values at which bluefish have relatively lower capture success (Fig. 3).

In 1994, there were four stations that had n>15 bay anchovy measurements for both spring and summer-spawned bluefish (n=16–20 bay anchovy measurements for summer- and n=22–39 for spring-spawned). Both spring- and summer-spawned YOY bluefish showed significant selection for relatively small bay anchovies (spring-spawned α=0.57 vs. 0.25, t=2.99, df=38, P=0.005; summer-spawned α=0.65 vs. 0.33, t=2.61, df=27, P=0.011) and avoidance of relatively larger anchovies in 1994 (spring-spawned α=0.02 vs. 0.25, t=3.83, df=38, P<0.001; summer-spawned α=0.07 vs. 0.33, t=2.86, df=27, P=0.006) (Table 7). Intermediate-size bay anchovy were taken in proportion to their abundance in 1994 (t-test; P>0.05 for all α's). In the 1995 analysis, three stations had n>15 individual bay anchovy lengths (n=17–32); an analysis of size-selective feeding of summer-spawned fish in 1995 was not possible owing to small sample size. Spring-spawned bluefish in 1995 showed no significant size selectivity (t-test; P>0.05 for all α's); however, the trend of increasing selectivity with decreasing prey sizes was present (Table 7).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Both spring- and summer-spawned YOY bluefish gut fullness values varied over the diel cycle in the different geographical regions of the MAB shelf. Peaks in gut fullness generally occurred at dawn, dusk, and diurnal time periods, whereas gut fullness values during nighttime collections were low in relation to diurnal gut fullness values (Fig. 4).

Table 7

Size-selectivity (Chesson's α, see text for calculations) for bay anchovy in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of $\alpha = 1/m$ (where "m" is the number of prey categories) represent random feeding while values of $\alpha > 1/m$ or $\alpha < 1/m$ represent "selection" and "avoidance" of prey, respectively. Values significantly different from $1/m$ (t-test, $P<0.05$) are indicated by a (+) for "selection" or (–) for "avoidance".

	1994		1995	
Bay anchovy size (mm)	Spring-spawned ($1/m$=0.25)	Summer-spawned ($1/m$=0.33)	Spring-spawned ($1/m$=0.33)	Summer-spawned
25–34	0.57 (+)	0.65 (+)	—	—
35–44	0.27	0.28	0.44	—
45–54	0.14	0.07 (–)	0.37	—
55–64	0.02 (–)	—	0.19	—

In order to use the gut fullness data to estimate bluefish daily ration, gastric evacuation rate (GER) estimates were needed for bluefish at shelf water temperatures. The exponential GER model adequately described the evacuation of bay anchovy at 15°C from our laboratory experiment (r^2=0.87, n=22, $P<0.001$; Fig. 5). Incorporation of the 15°C GER estimate (R_e=0.102) into the evacuation rate vs. temperature function of Buckel and Conover (1996) gave the following equation: $R_e = 0.017\ e^{0.099\ Temp}$, n=16, r^2=0.82 (Fig. 5). The largest deviation from the equation describing R_e and temperature is from the single estimate of GER at 15°C. This is likely not due to differences in experimental protocol; the 15°C GER experiment was conducted identically to the experiments described in Buckel and Conover (1996). The larger deviation may result from there being only one estimate of GER at 15°C whereas each GER estimate for the higher temperatures represents a mean of four estimates (Fig. 5). Estimates of GER from this equation were used to estimate bluefish daily ration.

The daily ration of summer-spawned bluefish in the SNE region in 1994 and 1995 was 8.5 and 12.4 g/(g · d) · 100, respectively (Table 8). Spring-spawned bluefish daily ration estimates ranged from 4.8 to 6.6 g/(g · d) · 100 for the SNE and C–D region in 1994 and 3.7–9.0 g/(g · d) · 100 in the SNE, C–D, and SOC regions of the MAB in 1995. There was insufficient diel records to calculate feeding rates for the SOC region in 1994 or the remaining region and cohort combinations (Table 8).

Table 8

Daily ration g/(g · d) · 100 ±SE) and weighted mean temperature at which spring- and summer-spawned YOY bluefish were collected during National Marine Fisheries Service autumn bottom trawl survey in 1994 and 1995. Bluefish juveniles were collected from three geographical areas of the Middle Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC= South of Chesapeake Bay, after Munch 1997). Daily ration was calculated using the Eggers' (1979) approach (see text). NA=not applicable due to low number of samples for diel series.

	Summer-spawned			Spring-spawned		
Year and geographical region	n	Temp. C	Daily ration g/(g · d) · 100 (SE)	n	Temp. C	Daily ration g/(g · d) · 100 (SE)
1994						
SNE	200	18.9	8.5 (3.1)	182	18.8	6.6 (2.5)
C–D			NA	129	20.0	4.8 (1.9)
1995						
SNE	61	20.7	12.4 (3.9)	79	19.9	3.7 (1.4)
C–D			NA	177	23.7	9.0 (2.9)
SOC			NA	51	24.3	8.1 (2.8)

The VPA estimates of YOY bluefish abundance in 1994 and 1995 were 24 million and 14 million, respectively. These estimations were partitioned into spring- and summer-spawned bluefish on the basis of relative abundances of these cohorts for each year (Table 9). It was estimated that spring-spawned bluefish consumed from 70 to 96 million bay anchovy per day in 1994 and from 68 to 170 million bay anchovy per day in 1995 during the September period of their migration (Table 9; the range is based on the lowest to highest daily ration estimate). Summer-spawned bluefish consumed 130 million bay anchovy per day in 1994 and 5 million per day in 1995 (there is no range for summer-spawned bluefish because there

was only one estimate of summer-spawned daily ration for each year).

Discussion

Dietary analyses

Bay anchovy was the predominant fish prey of both spring- and summer-spawned YOY bluefish in both 1994 and 1995. A previous gut contents analysis of NEFSC-NMFS bottom-trawl-collected bluefish (south of Cape Hatteras to Georges Bank) was conducted by Morris[2] from 1978 to 1980. Bay and striped anchovy dominated the diet of the 292 YOY bluefish (110–300 mm) that he examined; butterfish and squid were also important prey. The migration of YOY bluefish onto the shelf is thought to be controlled by declines in estuarine temperature and day length (Olla and Studholme, 1972). Schools of bay anchovy migrate out onto the shelf beginning in September and are concentrated off New York, New Jersey, and the Delmarva peninsula in the autumn (Vouglitois et al., 1987) in a similar pattern to that of concentrations of YOY bluefish (Munch and Conover, in press). The timing of bluefish estuarine emigration may be linked with bay anchovy movements offshore.

Invertebrates were an important part of the diet of YOY bluefish in several regions. In 1994, there was a large amount of gammarid amphipods in the diets of spring- and summer-spawned bluefish in the SNE region. In addition, mysids contributed to the diet of summer-spawned fish in the C–D and SOC regions of the continental shelf in 1994. Diets of juvenile bluefish in estuaries are usually dominated by fish prey, but at times invertebrates, such as shrimp, are a major prey (Friedland et al., 1988; Juanes and Conover, 1995). This pattern is likely a function of prey availability and prey size. Bluefish prey selectivity was related to prey abundance in the Hudson River (Buckel et al., 1999). Bay anchovy schools and invertebrate swarms are likely to have patchy distributions on the shelf; the diet of bluefish at any location will be dependent on local prey availability.

Channeled whelk has not been reported previously as a prey of bluefish. The foot of channeled whelk with the operculum still attached was found in several bluefish in the C–D region in 1995. This may have been due to opportunistic feeding on whelk that had shell damage related to some fishery activity. However, whelk occurred in bluefish gut contents over a fairly broad geographic area and not at a single

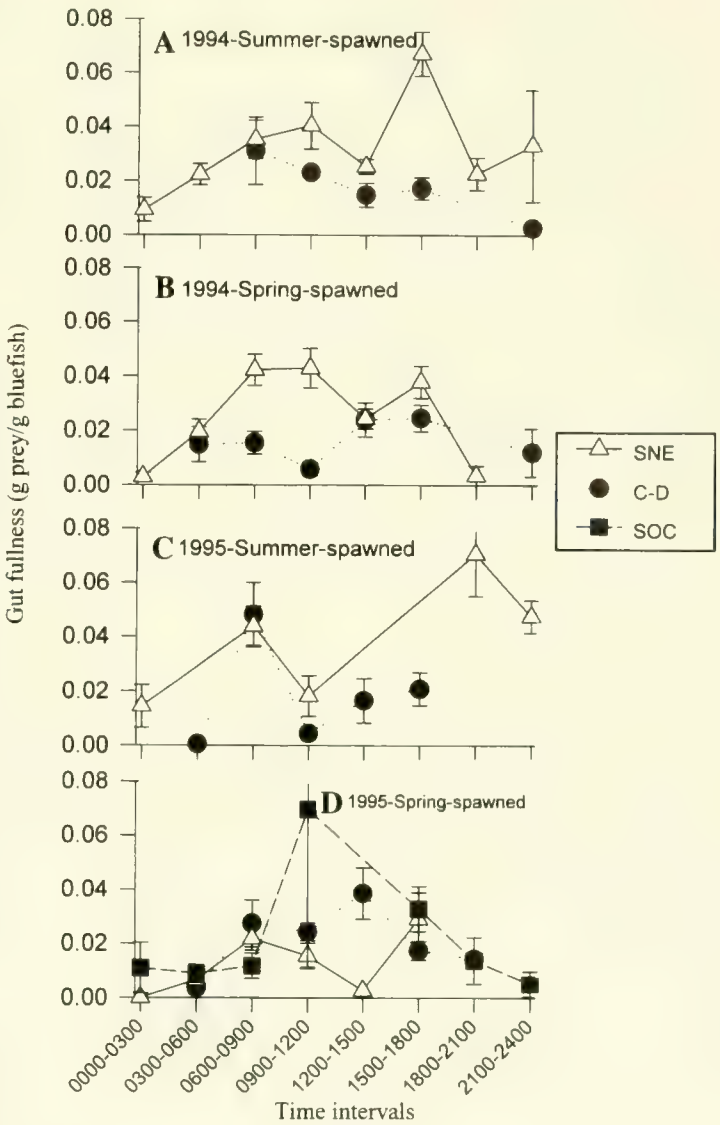

Figure 4

Gut fullness (g prey/g bluefish) for spring-and summer-spawned bluefish collected from SNE, C–D, and SOC regions of the continental shelf in 1994 (**A, B**) and 1995 (**C, D**) versus time interval of collection. Sunrise fell between the 0600 and 0900 time interval and sunset fell between the 1800 and 2100 time interval. Error bars are ±1 SE.

[2] Morris, T. L. 1984. Food of bluefish. Woods Hole Laboratory Reference Document 84-22, Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543 MED/NEFC 84-26, 13 p.

station (Cape May, NJ, to Lewes, DE). Bluefish may attack whelk when the foot is extended out of the shell and may sever that section alone. This would explain the presence of only the foot portion of the animal.

Summer-spawned bluefish diet was dominated by copepods in the SNE region in 1995. Marks and Conover (1993) found that the diet of summer-spawned bluefish collected in surface waters of the New York Bight was dominated by copepods. Summer-spawned bluefish size ranged from 17 to 64 mm TL in their samples and ranged from 20 to 140 mm FL in our samples from the SNE region in 1995. The large presence of copepods in this cohort's diet compared with other regions on the shelf in 1995 and with summer-spawned bluefish diets in 1994 is most likely a result of their small size (see "Prey-size analysis" section).

McBride et al. (1995) found that age-0, spring-spawned bluefish abundance appeared to be regulated by density-dependent (compensatory) losses in Narragansett Bay, Rhode Island. One potential density-dependent mechanism is cannibalism. There were very few cases of bluefish cannibalism on the continental shelf; spring-spawned bluefish cannibalism of summer-spawned bluefish occurred in the C–D and SOC region in 1995, a year when individuals in the summer-spawned cohort were relatively small in size. However, past diet studies of bluefish have found a higher incidence of cannibalism, particularly off the Carolinas (Lassiter, 1962; Naughton and Saloman, 1984). Bluefish abundance is currently low (NEFSC[1]) and cannibalism may be frequent only when bluefish are more abundant or other prey abundances are low.

We found slight regional differences in the diet of adult bluefish; diets of bluefish in 1994 and 1995 were similar to those found in past studies. In the Georges Bank region in 1994 and 1995, the dominant prey of adult bluefish were butterfish, long-finned squid, boreal squid, round herring, and Atlantic herring. Bay anchovy, butterfish, round herring, and long-finned squid were the dominant prey of adult bluefish collected from Cape Hatteras, NC, to Montauk Point, NY. Morris (1984) found that long-finned squid, boreal squid, butterfish, round herring, and bay and striped anchovies dominated the diet of adult bluefish (n=226) captured in NEFSC-NMFS bottom trawls (1978–80, spring, summer, autumn combined) from these same regions. Richards (1976) examined the diet of adult bluefish angled near Long Island, NY, in the summer and autumn. The diet of bluefish in this area included bay anchovy, long-finned squid, menhaden (*Brevoortia tyrannus*), butterfish, and silver hake (n=66, FL range: 490–750 mm).

There were very few bluefish for our diet analysis from south of Cape Hatteras; however, Naughton and Saloman (1984) collected 729 bluefish from this region using hook and line during 1977–81 and reported the diet of bluefish in this area as dominated by Scianidae, Clupeidae, Mugilidae, Labridae, and Atherinidae. Scianids, clupeids, engraulids, sparids, atherinids, and squids were important prey in Lassiter's (1962) study of over 900 bluefish captured by beach haul seining or hook and line August–December 1960 and March, June–August 1961. The diet of bluefish (n=42) collected south of Cape Hatteras in the autumn by bottom trawling was dominated by squid, butterfish, and striped anchovy (Morris, 1984).

There were several commercially important groundfish species in the diet of adult bluefish on Georges

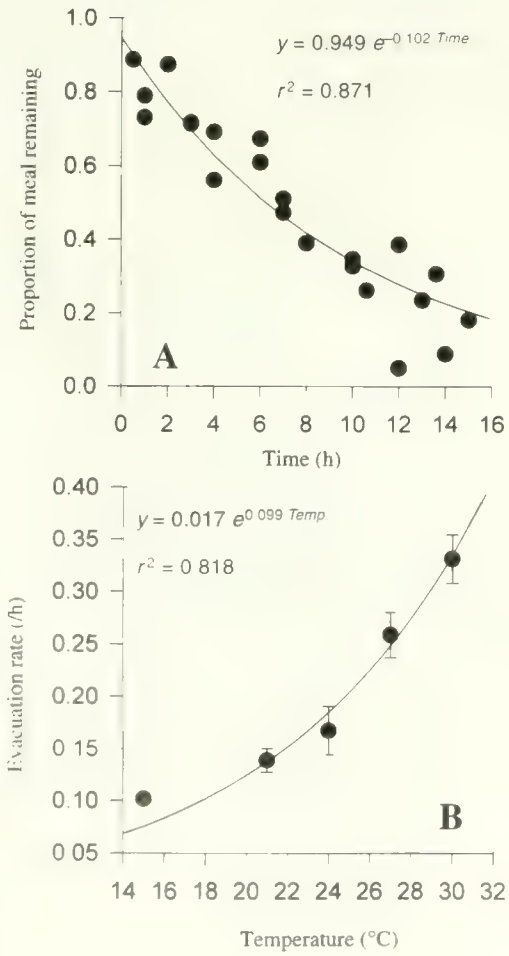

Figure 5

(**A**) Proportion of meal remaining vs. time for bluefish fed a single bay anchovy meal at 15°C (*proportion of meal remaining* = 0.949 $e^{-0.102 \cdot time}$, and (**B**) YOY bluefish evacuation rate versus temperature (data for temperatures of 21 to 30°C are from Buckel and Conover, 1996; *evacuation rate*=0.017$e^{0.099 \cdot temp}$). Error bars are ±1 SE.

Table 9

Estimated spring- and summer-spawned bluefish daily consumption of bay anchovy on the U.S. east coast continental shelf in the autumn of 1994 and 1995. We used mean size of bluefish, daily ration estimates, proportion of bay anchovy in the diet, and mean bay anchovy size that were measured for each cohort in this study. Estimates of the numbers of YOY bluefish for 1994 and 1995 are from virtual population analysis (VPA) performed by NEFSC (see Footnote 1 in main text); we partitioned the numbers between spring- and summer- spawned bluefish using relative abundances of each cohort from the NEFSC-NMFS autumn groundfish survey cruises.

Cohort	Bluefish numbers	Biomass of bluefish cohort (10^6 kg)	Amount of bay anchovy consumed daily (kg/d; low ration)	Amount of bay anchovy consumed daily (kg/d; high ration)	Number of bay anchovy consumed daily (no./d; low)	Number of bay anchovy consumed daily (no./d; high)
1994						
Total	24×10^6					
Spring-spawned	7.2×10^6	1.20	25,000	34,000	70×10^6	96×10^6
Summer-spawned	16.8×10^6	0.50	35,000		130×10^6	
1995						
Total	14×10^6					
Spring-spawned	9.8×10^6	1.86	45,000	110,000	68×10^6	170×10^6
Summer-spawned	4.2×10^6	0.032	2,000		5×10^6	

Bank in 1994. Morris (1984) also found gadids in stomach contents of adult bluefish. This finding is of interest because there is a large effort to understand the factors that regulate fish populations on Georges Bank (Peterson and Powell, 1991). The biomass of skates (Rajidae) and dogfish sharks (Squalidae) has increased in this area of the shelf and in some locations makes up the largest part of fish biomass (Overholtz et al., 1991). However, cartilaginous fishes were not found in the diet of adult bluefish. Bluefish predation will have no direct effect in regulating the population sizes of these fishes. However, bluefish may play a role in the recovery of commercially important groundfish species on Georges Bank. Because bluefish distribution is closely linked with temperature (Munch, 1997), an increased warming trend may allow a larger proportion of the bluefish population to extend northward onto Georges Bank. Ware and McFarlane (1995) found that Pacific hake (*Merluccius productus*) biomass and hake predation on herring (*Clupea harengus*) increased with recent increases in temperature off the west coast of Vancouver Island. They concluded that this recent increased predation explains recent declines in the herring stock. The importance of bluefish predation to recovery of groundfish species warrants further investigation.

Net feeding

Postcapture net-feeding can bias diet indices and gut fullness level estimates. Net feeding is known to occur in a variety of Pacific midwater fish (Lancraft and Robison, 1980). There was little evidence that net feeding biased our estimates of bluefish diet given the similarities between percent of fresh versus digested prey; however, any net feeding would lead to biased estimates of gut fullness level and inflated estimates of consumption rate. Lancraft and Robison (1980) found that larger fish were more likely to ingest artificial prey. The larger spring-spawned cohort had more fresh prey in its diet than the smaller summer-spawned bluefish which may be a result of a higher incidence of net feeding by this cohort.

Prey-type selectivity

Spring-spawned YOY bluefish selected for bay anchovy over all other prey types in both 1994 and 1995. Butterfish, squid, and "other" potential prey were avoided. This is most likely due to both the relative abundances of these prey as well as interspecific size differences. Bay anchovy tended to be the smallest prey available; the only smaller prey of spring-spawned bluefish were invertebrates such as amphipods (ranging from 3 to 15 mm TL). In the Hudson River estuary, the prey with the highest relative abundance were selected for, whereas the prey with the lowest abundance were selected against (Buckel et al., 1999). A second possible explanation for the strong selection of bay anchovy could be sampling bias. Chesson's (1978) index assumes that prey abundance is large in relation to the amount consumed (likely true for the shelf) and that the

catchability or availability of the different prey groups to the trawl are the same. We do not have estimates of the catchability for each of the prey species used in this analysis. Our results would be biased if these differ. For example, catchabilities for squid and butterfish may be higher than that of bay anchovy and may explain the strong selection for bay anchovy.

Prey-size analysis

Although there was a weak positive linear relationship between ingested bluefish prey sizes and bluefish length, it was mainly due to prey other than bay anchovy. The slope of the regression of bay anchovy length on bluefish length alone was 50% and 75% less than the slope of the regression of all prey on bluefish length in 1994 and 1995, respectively. The sizes of bay anchovy taken by the smallest YOY bluefish were similar to those taken by the largest YOY bluefish, especially in 1995. Juanes and Conover (1995) and Scharf et al. (1997) saw a similar relation for bluefish feeding on piscine prey in New York estuaries.

Most ratios of bay anchovy length to bluefish length were similar to those seen in past estuarine work (Juanes and Conover, 1995; Scharf et al., 1997). Juanes and Conover (1995) hypothesized that the shift in spring-spawned bluefish diet from Atlantic silversides to bay anchovy in Great South Bay, NY, was a result of the higher capture success on the relatively smaller bay anchovy. The capture success of bluefish feeding on bay anchovy is likely higher than that of bluefish feeding on the relatively larger butterfish and squid. Our size selectivity analysis shows that even within bay anchovy there is preference for smaller sizes (Table 7).

The relatively small size of the 1995 SNE summer-spawned bluefish (1994 mean FL=135 vs. 1995 mean FL=70) influenced the extent of piscivorous feeding in this cohort. The capture success was plotted for bluefish feeding at different ratios of prey length to bluefish length from laboratory work on Atlantic silversides (Scharf et al., 1998b). Summer-spawned, small-size bluefish in 1995 would have experienced greatly reduced capture success when feeding on bay anchovy.

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Bluefish appear to feed mainly during the day or at dawn or dusk. This was also noted in past work on juvenile bluefish in estuarine environments (Juanes and Conover, 1994; Buckel and Conover, 1997). In the Hudson River estuary, the diel feeding patterns of bluefish appeared to be linked to their diel movement patterns (Buckel and Conover, 1997). This may also be the case for shelf bluefish; Munch (1997) found that the catch per unit of effort (CPUE) of YOY bluefish in NEFSC-NMFS bottom trawl collections was significantly higher in diurnal than in nocturnal collections. Munch (1997) hypothesized that this diel movement to near bottom habitat (which makes them available to bottom trawling) during the day may be in response to the vertical migration of bay anchovy. Bay anchovy exhibit diel vertical migration and are significantly more available to bottom trawl sampling during the day compared with at night (Vouglitois et al., 1987).

Our daily ration estimates for spring-spawned bluefish (3.7–9.0 g /(g · d) · 100) are similar to past estimates of daily ration for September. Measurements of bluefish maximum daily ration from a laboratory mesocosm experiment (18.5–23°C) for mid-September were ~10 g/(g · d) · 100 (Buckel et al., 1995). Field estimates of bluefish daily ration in the Hudson River estuary were 10.1–12.6 in mid to late August and 7.3 in mid-September (Buckel and Conover, 1997). Mean spring-spawned bluefish size was larger and mean temperatures were slightly lower on the shelf compared with bluefish sizes and temperatures in the above laboratory and field experiments. This finding may explain our slightly lower daily ration estimates for spring-spawned bluefish on the shelf in the autumn. Hartman and Brandt's (1995b) laboratory estimates of maximum daily ration (C_{max}) are also similar to our field estimates of spring-spawned bluefish daily ration estimates on the shelf. From their experiments, estimates of C_{max} for bluefish ranging from 100 to 350 g at 20°C (temperature at which bluefish were found on the shelf) are 7.5 to 12.5 g/(g · d) · 100.

Owing to low sample sizes and an inadequate diel record, the daily ration of summer-spawned bluefish was determined only in the SNE region in 1994 and 1995. The daily ration estimate in 1994 was lower at 8.5 g/(g · d) · 100 than the estimate of 12.5 g/(g · d) · 100 in 1995. The mean size of fish in this cohort varied substantially between 1994 (31.2 g) and 1995 (4.8 g). The size and the temperature difference (1994= 18.9°C vs. 1995=20.7°C) may explain the differences in daily ration. The daily ration estimates of these fish are slightly lower than would be predicted from laboratory estimates of maximum daily ration of bluefish at these sizes and temperatures (Buckel et al., 1995; Hartman and Brandt, 1995b); however, both shelf estimates fall into the 95% confidence interval of the summer-spawned bluefish daily ration estimate (19–20 September 1992) in the Hudson River (Buckel and Conover, 1997).

For our estimates of bay anchovy consumption by the YOY bluefish population during their September migration, it was assumed that the entire YOY bluefish population occurred on the shelf from Cape Hatteras, NC, to Montauk, NY. Support for this comes from sharp declines in YOY bluefish CPUE in early autumn estuarine beach seine surveys (Nyman and Conover, 1988; McBride and Conover, 1991) and an abrupt decline in average bluefish size on the shelf during early autumn (Munch, 1997). Our estimates show that given a 30-d migration period in September, the population of YOY bluefish could consume from 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995.

Summer-spawned bluefish consumed two orders of magnitude less bay anchovy per day in 1995 (5 million) compared with 1994 (130 million). This was partly due to the low abundance of this cohort in 1995 (4.2 million) compared with that in 1994 (16.8 million). The amount of bay anchovy in the diet of summer-spawned bluefish (80% in 1994 vs. 60% in 1995) and the absolute size of bay anchovy prey taken by the two cohorts (0.27 g in 1994 vs. 0.54 g in 1995) explained the remainder. Interannual variation in the size structure of the summer-spawned cohort and their predominant piscine prey (bay anchovy) can have dramatic effects on the predatory impact of this bluefish cohort on bay anchovy populations. Although the importance of size-dependent processes in freshwater fish predator-prey interactions is well described (Kerfoot and Sih, 1987; Ebenman and Persson, 1988), their importance for piscivore-prey interactions in marine systems is just beginning to be recognized (Juanes and Conover, 1995).

There are no estimates of coastwide bay anchovy abundance for 1994 and 1995; hence, no direct examination of the impact of this estimated bay anchovy loss to the continental shelf bay anchovy population was made. There are bay anchovy biomass density estimates for estuaries on the east coast of the U.S. Vouglitois et al. (1987) estimated that the bay anchovy standing crop in Barnegat Bay, NJ, ranged from 830 to 4830 kg/km^2. In Chesapeake Bay, Luo and Brandt's (1993) bay anchovy biomass density estimate for September was ~8000 kg/km^2. We calculated the standing stock of bay anchovy on the shelf by multiplying the estimated ranges of estuarine bay anchovy densities by the area (km^2) in which bluefish were collected on the shelf. This area (km^2) estimate was calculated by summing all the NEFSC stratum areas in which YOY bluefish were captured in the autumn groundfish survey in 1994 and 1995.

During the month of September, bluefish (spring- and summer-spawned combined) consumption of bay anchovy could account from ~2 to 22% of bay anchovy standing stock in 1994 and from 1% to 24% of the bay anchovy standing stock in 1995. Bay anchovy are probably less dense on the shelf than in the estuary and our estimates of bluefish impact may be underestimates. However, the latest bluefish stock assessment (Mid-Atlantic Fishery Management Council[3]) has found that bluefish abundance may be lower than that reported in the VPA (NEFSC[1]). This could mean that our impact estimates are overestimates. At the upper range of the impact estimates, it is clear that the YOY bluefish population on the continental shelf consume a significant quantity of bay anchovy biomass. The effect of this loss on the population dynamics of bay anchovy or the fish community on the continental shelf is unknown.

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[3] Mid-Atlantic Fishery Management Council. 1998. Amendment 1 to the bluefish fishery management plan, 340 p. [Available from Mid-Atlantic Fishery Management Council, Room 2115, Federal Building, 300 South New Street, Dover, DE 19904-6790.]

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Abstract.—The bluefish, *Pomatomus saltatrix*, has long been considered a key predator on U.S. east coast fish species. Many of its prey species are also landed by humans, but no comparison of prey biomass harvested by bluefish versus fishermen has been attempted previously. We used data on growth, mortality, gross growth efficiency, and abundance to model the total prey consumption rate by bluefish at the population level. This estimate and previously published information on diet were used to calculate the biomass of individual resource species "harvested" by bluefish. The prey biomass consumed by bluefish annually along the U.S. Atlantic coast is equal to eight times the biomass of the bluefish population. Bluefish consume a much higher biomass of squid and butterfish than is currently harvested by commercial fisheries for these species. Bluefish consumption of Atlantic menhaden, however, was below the current fisheries landings for this species. For resource species that are shared with bluefish, our findings highlight the need for multi-species assessment and management.

Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries*

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The bluefish, *Pomatomus saltatrix*, has long been regarded as one of the most voracious piscivores of the western North Atlantic. In 1873 the U.S. Commissioner of Fisheries, S. F. Baird, stated in a report to congress that: ". . . I am quite inclined to assign to the bluefish the very first position among the most injurious influences that have affected the supply of fishes . . . a daily loss of 25 hundred million pounds . . . their trail is marked by fragments of fish and the stain of blood . . ." (Baird, 1873). Baird was concerned with the possibility that the high abundance of bluefish during that period was the cause of concomitant declines in fish landings.

Bluefish abundance along the U.S. Atlantic coast has been known to fluctuate dramatically over the past two centuries (Bigelow and Schroeder, 1953). The impact of variations in bluefish abundance on their principal prey as well as on the community structure of the continental shelf as a whole may be substantial (Clepper, 1979; Kerfoot and Sih, 1987). If the major prey of bluefish are also harvested by humans, then the potential fishery landings of such species may be influenced strongly by bluefish abundance. Moreover, species management through adjustment of the fishing effort will likely be ineffective if the amount of prey consumed by a key natural predator is substantially larger than the landings and ignored as a variable component of natural mortality.

In this study, we estimate the total prey biomass consumed annually by a given biomass of bluefish using a model developed by Pauly

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(1986). Previously published data on diet and recent estimates of bluefish population size along the U.S. Atlantic coast were used to determine the "harvest" of prey by bluefish. We then compared "harvesting" of prey by bluefish to the biomass harvested by the fishery for the east coast as a whole. Prey consumption by age class was calculated to determine at which age the largest impact on prey occurs. We present these analyses not as management tools but merely as gross estimates of the probable magnitude of the bluefish harvest of fishery species so as to stimulate more detailed studies.

Methods

Estimates of population consumption rate

The total U.S. east coast bluefish population consumption of a given prey was calculated from estimates of diet, the biomass of the bluefish population, and food consumption rate. Bluefish diet information was available from the literature for various seasons and regions along the east coast (Lassiter, 1962; Richards, 1976; Buckel et al., 1999a; Morris[1]; Naughton and Saloman[2]). Bluefish biomass estimates were available for 1982 to 1995 from a virtual population analysis (VPA) performed by the Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, MA (NEFSC[3]). However, estimates of bluefish consumption rate were available only for young-of-the-year (YOY) (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1997) or for age-0 to age-2 bluefish in Chesapeake Bay (Hartman and Brandt, 1995a). For this reason, we used the approach described below.

The quantity of food consumed annually by the bluefish population was estimated by using Pauly's (1986) age-structured consumption rate model. The model is based on a growth function (e.g. von Bertalanffy growth function, VBGF), the instantaneous total mortality rate (Z), and the relationship of gross growth efficiency to weight. Pauly's (1986) model in simplified form is

$$\frac{Q}{B} = \frac{\int_{t_r}^{t_{max}} (dw/dt) \times N_t \, dt \,/\, K_{1t}}{\int_{t}^{t_{max}} W_t \times N_t \, dt},$$

where Q/B is the food consumption per unit population biomass (see descriptions in Pauly (1986), Pauly and Palomares (1987), and Palomares and Pauly (1989)). The numerator of the model represents the food consumption of the population (Q), which is determined from the growth increment (dw/dt), numbers of fish at age t (N_t, determined from an initial arbitrary number of recruits), and the growth efficiency (K_1) for a given weight at age t. Values are integrated over age classes from t_r to t_{max} (age at recruitment to a maximum age). The denominator is the biomass term (B) which is the weight of individual fish at age t (W_t) multiplied by the number of fish (N_t) at age t. This value is integrated over all cohorts from t_r to t_{max}. An annual Q/B estimate represents the number of times the population consumes its own weight per year (Pauly, 1986).

Pauly and Palomares (1987) have provided a BASIC program to calculate Q/B from VBGF parameters, a parameter from the relationship describing K_1 as a function of weight, and an estimate of total mortality (Z). Growth for the Q/B model is based on the VBGF model expressed in weight form:

$$W_t = W_\infty \times \left[1 - e^{-k \times (t - t_0)}\right]^b,$$

where t = time in years;
W_t = weight of bluefish at age t;
W_∞ = asymptotic weight;
k = growth coefficient;
t_0 = age at weight zero; and
b = exponent of the length-weight relationship (i.e. $W=aL^b$).

For bluefish, Wilk's (1977) VBGF parameters were used where $k = 0.226$, $t_0 = -0.123$, $W_\infty = 8725$g, and $b = 3$ (Wilk's estimate of b was 2.89 but $b = 3$ was used owing to ease of use in Pauly's (1986) model).

The Q/B model assumes that gross growth efficiency (K_1) data depends on weight (W) according to

$$K_1 = 1 - (W/W_\infty)^\beta$$

To estimate β for use in the calculation of Q/B, bluefish gross growth efficiency and weight data from experiments on YOY fish described in Buckel et al. (1995) were used. The linearized form of the above model described in Pauly (1986) was fitted to the data

[1] Morris, T. L. 1984. Food of bluefish. Woods Hole Ref. Doc. 84-22, 13 p. [Available from Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543.]

[2] Naughton, S. P., and C. H. Saloman. 1984. Food of bluefish (*Pomatomus saltatrix*) from the U.S. south Atlantic and Gulf of Mexico. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-150, 37 p.

[3] NEFSC (Northeast Fisheries Science Center). 1997. Report of the 23rd Northeast Regional Stock Assessment Workshop (23rd SAW) Stock Assessment Review Committee (SARC) consensus summary of assessments. Northeast Fisheries Sci. Cent. Ref. Doc. 97-05, 105 p.

to estimate β (β=–0.0445, r^2=0.64, F=45.44, df=1,25, P<0.0001).

The current stock assessment of bluefish assumes a natural mortality of M=0.25. The highest fishing mortality (F) measured on the east coast bluefish population was in 1992 at 0.51 and recent estimates of F are around 0.4–0.5 (NEFSC[3]). Therefore, an estimate of $M + F$=0.75 was used as a total mortality (Z) input into the Pauly (1986) model to estimate Q/B. The value of Z does not affect the estimate of Q/B dramatically because of its presence in both the numerator and denominator of the equation (see above). Annual consumption (Q/B) was estimated for bluefish from age-0 to age-10.

To determine if our estimate was robust, Hartman and Brandt's (1995a) equation ($C_{max} = 0.520 \times W^{-0.288}$) describing laboratory (20–25°C) estimates of maximum consumption rate (C_{max}, g/(g · d)) as a function of bluefish weight (W, g) was also used to calculate the population consumption for 1995. First, bluefish biomass by age class was calculated by multiplying bluefish numbers at age (NEFSC[3]) by the mean bluefish weight at age (W_t calculated from Wilk's (1977) VBGF function and length:weight conversion equation; $W_{age\,0}$ was estimated at t=0.5). Second, the maximum consumption rate was calculated for a mean bluefish weight at age from the relationship between C_{max} and bluefish weight provided by Hartman and Brandt (1995a). To do so, we extrapolated out beyond the range of fish sizes used in their laboratory experiment, assuming that values obtained in this way were accurate. Lastly, these age-specific consumption rates were then multiplied by the biomass of each age class. Summing across age classes provided us with a maximum biomass of prey consumed by the bluefish population at 20–25°C; this value was divided by the biomass of the population to obtain a daily Q/B value. To calculate an annual Q/B value, the daily Q/B value was multiplied by 365 days. Additionally, this Q/B value was temperature adjusted from 22.5°C to 17.5°C. This was done by multiplying by the ratio of bluefish consumption rate estimated at 17.5°C (average temperature for coastal bluefish [Munch, 1997]) to consumption rate estimated at 22.5°C (temperature of Hartman and Brandt's [1995a] study). This ratio was estimated from both Buckel et al. (1995) and Hartman and Brandt (1995a) data and in both cases was found to be ~0.60.

Impact by age class

From the above analysis, the age class where total biomass consumption peaks can be determined. This calculation was first made for a simulated bluefish population having constant recruitment (N=1 × 10^7) and total mortality (Z=0.75, see above). However, bluefish exhibit highly variable recruitment across years. To illustrate the impact of variable age structure, we also calculated biomass consumed by age class on the basis of actual abundances in 1984 (a year when preceding recruitments had been fairly constant and age structure was typical) and in 1995 (a year when preceding recruitments were highly variable and age structure was unstable).

Comparison of biomass consumed by bluefish with that harvested by fisheries

The estimate of the annual amount of prey consumed by the western Atlantic bluefish population is the annual Q/B estimate (described above) multiplied by stock biomass. The prey consumption for three different population biomass sizes was estimated based on VPA estimates; these were the minimum, maximum, and average population sizes from 1982 to 1995 (NEFSC[3]). The total annual consumption at these three stock sizes was estimated for Atlantic butterfish (*Peprilus triacanthus*), long-finned squid (*Loligo pealei*), boreal squid (*Illex illecebrosus*), and Atlantic menhaden (*Brevoortia tyrannus*). These are primary species in the diet of bluefish that are also landed by fishermen.

Several studies were used to attribute the total biomass consumption by bluefish to different geographic regions, seasons, and prey species. To simulate the migratory patterns of bluefish, it was assumed that 100% of the population was north of Cape Hatteras during summer and autumn and 100% of the population was south of Cape Hatteras during spring and winter. Diet data from Richards (1976), Morris[1], and Buckel et al. (1999b) were used to describe bluefish diet in the summer and autumn north of Cape Hatteras. The diet studies of Naughton and Saloman[2] and Lassiter (1962) were used to describe bluefish diet south of Cape Hatteras (Carolinas and southeast Florida) during winter and spring. Details regarding these diet studies can be found in Buckel et al. (1999b).

To calibrate the relative importance of bluefish predation on squid, butterfish, and menhaden, the annual bluefish consumption of these prey was plotted along with the average, minimum, and maximum fisheries landings (1984–92) for these species as compiled by the National Marine Fisheries Service (Anonymous[4]).

[4] Anonymous. 1993. Fisheries of the United States, 1992. U.S. Dep. Commer., National Oceanic and Atmospheric Association, National Marine Fisheries Service, Silver Spring, MD, 115 p.

Table 1

Estimate of daily and annual prey consumption of the 1995 bluefish population by age class. We used weight-at-age data from Wilk,[1] maximum consumption rate estimates from Hartman and Brandt (1995a), and the virtual population analysis (VPA) estimates of bluefish number by age from NEFSC (see Footnote 3 in main text).

Age	Bluefish weight (kg)	Bluefish numbers (millions)	Bluefish biomass (10^6 kg)	Consumption rate (kg/(kg · d))	Biomass of prey consumed daily (kg)
0.5	0.031	13.89	0.43	0.1941	82538
1	0.143	17.47	2.50	0.1245	311317
2	0.662	4.78	3.16	0.0801	253240
3	1.502	3.95	5.92	0.0633	374750
4	2.524	2.86	7.22	0.0545	393250
5	3.604	3.31	11.92	0.0492	585820
6	4.654	5.88	27.35	0.0456	1249322
7	5.622	2.76	15.53	0.0432	671889
8	6.481	1.55	10.03	0.04152	416561
9+	7.225	3.99	28.84	0.0402	1160642
		Sum of bluefish biomass (B; 10^6 kg)	112.90	Sum of biomass consumed (Q; kg)	5499328
				Q/B daily (at 22.5°C)	0.0487
				Q/B annual (at 22.5°C)	17.78
				Q/B annual (at 17.5°C)	10.84

[1] Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Tech. Ser. Rep. 11, 56 p. [Available from James J. Howard Marine Sciences Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 74 Magruder Rd., Highlands, NJ.]

Effects of pooling diet across ages

One potential shortcoming of this analysis was the use of diet data pooled across age or size groups. This procedure was unavoidable because of the lack of data describing bluefish diet by age or size for different seasons and geographical locations on the east coast of the United States. The use of pooled diet data may bias impact estimates given that prey such as squid, butterfish, and squid are more important diet items of older and larger bluefish. To address this potential bias, we performed a separate analysis to calculate bluefish consumption of prey using size or specific diet data (where available, see Morris[1]) as opposed to pooled data. The daily biomass of prey consumed by each age or size class (uncorrected for temperature) was calculated for the simulated population (a population with constant recruitment and mortality, see "Estimates of population consumption rate" section) and the 1995 bluefish population (a population whose biomass was dominated by older fish, see "Impact by age class" section and Table 1). These consumption-by-age estimates were multiplied by percent-contribution-by-weight data from Morris[1] for the four prey species described in the main analysis. The biomass of each prey type that was consumed was summed over all age classes to obtain the population consumption of each prey type. These values were then compared with values of population consumption of each prey type that were obtained by multiplying the total population consumption of all prey by the pooled prey contribution from Morris.

Results

Estimates of population consumption rate

The annual Q/B estimate from Pauly's (1986) model for the east coast bluefish population is 7.7. This means that the east coast bluefish population consumes a biomass of prey that is equivalent to ~8 times its own biomass over a one year period. The estimate of Q/B with Hartman and Brandt's (1995a) consumption-rate-at-weight data, adjusted for temperature, and estimated for the 1995 bluefish biomass on the U.S. east coast, was 10.8 (Table 1).

Impact by age class

For the simulated population with constant recruitment and mortality, the peak predatory impact of the bluefish population occurs between approximately age 1 and age 3 (Fig. 1). In 1984, a year with

fairly typical age structure, peak absolute consumption of prey occurred between age 2 and age 3 with a second peak at age 6 (Fig. 2). In 1995, when age structure was dominated by the 1989 year class, peak predatory impact occurred in fish that were six years of age (Table 1; Fig. 3). Therefore, much interannual variation in the age classes at which the peak predatory impact occurs should be expected in bluefish.

Comparison of biomass consumed by bluefish with that harvested by fisheries

The bluefish VPA biomass estimates from 1982 to 1995 ranged from a low of 124,024 metric tons (t) in 1995 to a high of 328,864 t in 1986 with an average stock size of 233,309 t for this period (NEFSC[3]). Given a Q/B estimate of 7.7, the minimum-size bluefish

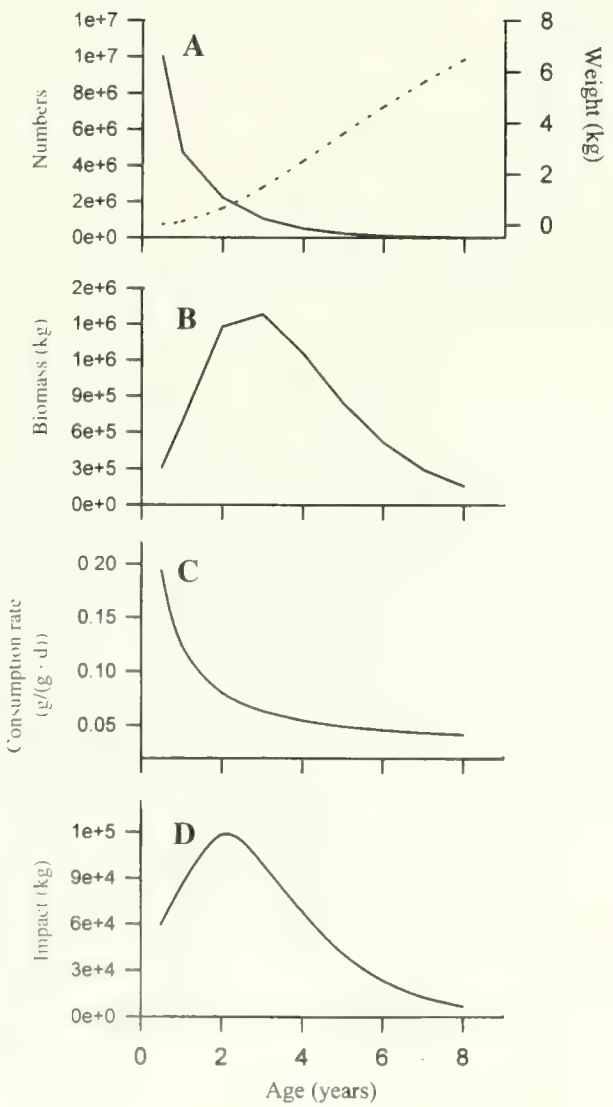

Figure 1

Estimates of bluefish impact on prey by age class for a simulated population of the U.S. east coast bluefish stock. Simulated numbers of bluefish (see text) and bluefish weight (kg; Wilk,1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).

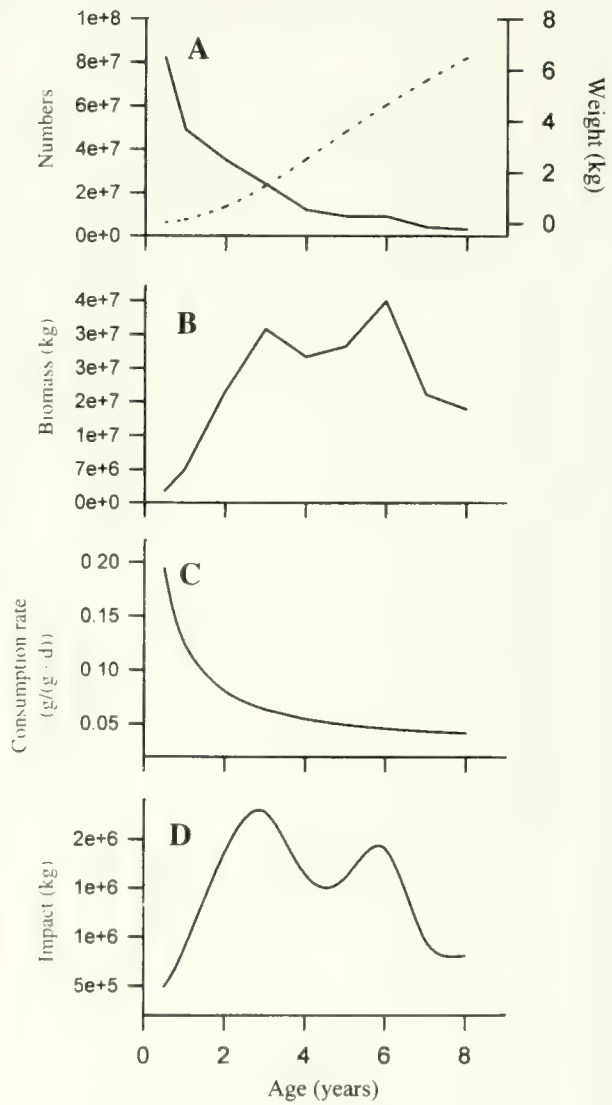

Figure 2

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1984. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by the maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).

population (1995) consumed 0.9 million t per year whereas the maximum-size population (1986) consumed 2.5 million t of prey per year. The 1982 to 1995 average population biomass consumed 1.8 million t of prey per year.

Of the total biomass of prey consumed annually by bluefish, the fraction attributed to the primary resource species is an annual average of 10% butterfish, 10% long-finned squid, 5% boreal squid, and 5% Atlantic menhaden. These are also averages across bluefish body size; however, these averages may be too simplistic given that bluefish diet changes with increasing size. Much of the rest of the diet of bluefish is attributed to bay anchovy (described in Buckel et al., 1999a) for which no fishery landings exist. The average (minimum-maximum) annual consumption of butterfish by bluefish is therefore 90,000 t (48,000–125,000 t); annual consumtion of long-finned squid, is 90,000 t (48,000–125,000 t); and annual consumption of boreal squid, is 45,000 t (24,000–63,000 t). The annual consumption of these species by bluefish is much higher than the annual fisheries landings over the period 1984–92 (Fig. 4). The average consumption of Atlantic menhaden by bluefish was 45,000 t (24,000–63,000 t). The menhaden fishery takes seven times the biomass of menhaden that bluefish consume (Fig. 4).

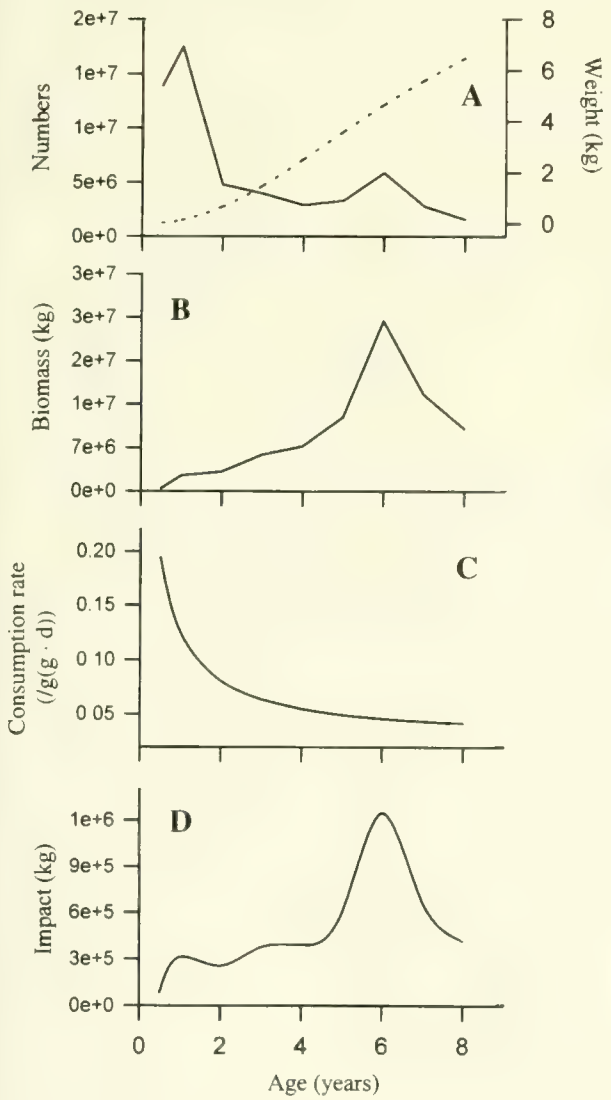

Figure 3

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1995. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt 1995a) for each age class (**C**).

Effects of pooling diet across ages

For the simulated population, the daily consumption of long-finned squid and butterfish calculated by using age-specific data did not differ greatly from daily consumption when diets were pooled across ages (Fig. 5). However, the use of pooled diets overestimated daily consumption of boreal squid and Atlantic menhaden in comparison to values obtained with age-specific diets for both the simulated and 1995 bluefish population. For the 1995 population, age-specific diets gave daily consumption values for long-finned squid and butterfish that were higher than those that were calculated when pooled percent diet contributions were used (Fig. 5). Therefore, pooling diets can lead to under- or over-estimates of the predation pressure by bluefish; this bias can be affected by the age structure of the bluefish population.

Discussion

The results suggest that for at least three of the prey species of bluefish and humans, bluefish harvest a much higher biomass than does the fishery. This predatory loss will vary with fluctuations in bluefish abundance. We elaborate on management implications below.

Estimates of population consumption rate

Our estimate of Q/B (annual population consumption) is likely robust for two reasons. First, the estimate of bluefish annual Q/B is similar to that of other pelagic piscivores. Palomares and Pauly (1989) esti-

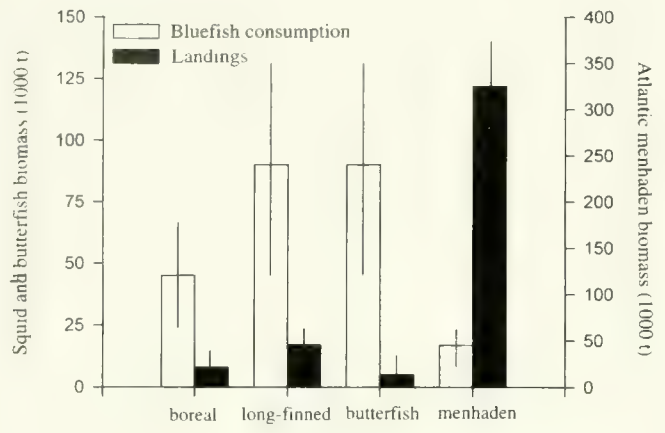

Figure 4

Estimated biomass (in thousands of metric tons (t)) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden consumed by the U.S. east coast bluefish population (open histogram represents consumption by average bluefish biomass from 1982 to 1995, error bar represents range for consumption by a minimum to maximum bluefish population size) and harvested by east coast fisheries (closed histogram represents average harvest from 1984 to 1992, error bar represents range for harvest from minimum to maximum).

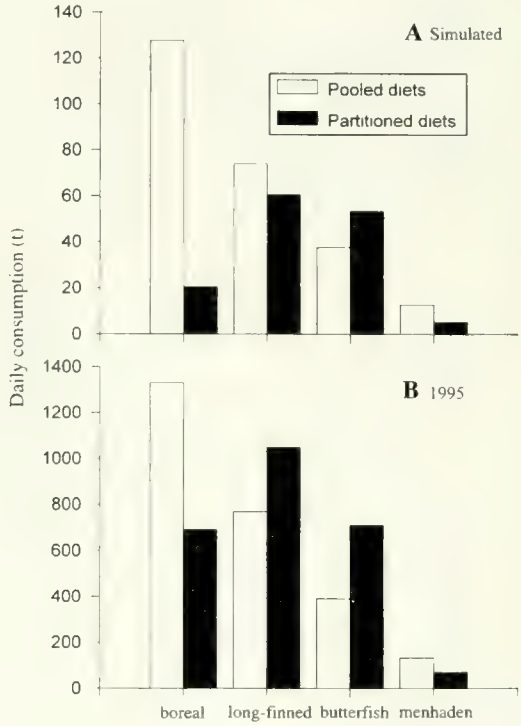

Figure 5

Daily consumption (not temperature corrected; t) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden by the U.S. east coast bluefish population based on simulated (**A**) and 1995 (**B**) data (see text for calculation methods). Consumption was estimated from pooled diet indices (open histogram) and indices which were partitioned by age or size (closed histogram).

mated the annual Q/B of bar jack, *Caranx ruber*, and the dolphin *Coryphaena hippurus* at 10.6 and 8.5, respectively. Secondly, the estimate of Q/B with laboratory-measured daily rations (age 0–2 yr fish) and 1995 VPA bluefish biomass data gave us an estimate of Q/B of 10.8. This value was only slightly higher than the estimate from Pauly's (1986) model. This difference is likely a result of extrapolating C_{max} data from Hartman and Brandt (1995a) to larger fish. Assuming consumption rates of these larger fish were overestimated, values of 2.0 to 3.0 kg/(kg · d) · 100 were substituted for fish ages 4–9+. From this a Q/B value of 6.6 was estimated. This value is more similar to the Pauly model Q/B estimate of 7.7. Future estimates of bluefish population consumption should include laboratory or field estimates of feeding rates of older bluefish.

The Q/B estimate based on the 1995 VPA (10.8) incorporates the age structure existing at that time (recruitment not constant in the population), whereas the estimate from Pauly's (1986) model (7.7) assumes constant recruitment. Age structure may also contribute to the differences between the two Q/B estimates. For the 1995 bluefish stock, recent years of low recruitment have led to peak biomass in the older age classes (NEFSC[3]). These older, more abundant age classes consume a higher biomass of prey than younger age classes. In 1995, age-6 fish consumed more prey biomass than any other age class. This strong age class resulted from a relatively large recruitment in 1989. If recruitment and mortality are constant, our analyses predict that absolute prey consumption will peak at about age 2 (Fig. 1D). That consumption rate tends to peak in the earlier age classes has also been found in other species (Stewart and Binkowski, 1986; Yañez-Arancibia et al., 1993).

Bluefish ingest larger and a greater diversity of prey and include more resource species in their diet (e.g. butterfish, squid, Atlantic herring, and several groundfish species), with increasing body size (Buckel et al., 1999b; Morris[1]). When coupled with temporal shifts in the biomass age structure of bluefish, such ontogenetic changes in diet have important implications for impact on prey populations. For example, bluefish recruitment was relatively high from 1982 through 1984. In 1984, peak absolute consumption of prey occurred between age 2 and 3 compared with age 6 in 1995. In 1984, the biomass consumption of age-0 through age-3 fish was 40% of the entire

population's consumption, but it was only 18% of total population consumption in 1995 (Figs. 2 and 3). Similarly, Hartman and Brandt (1995b) found that relative prey consumption by bluefish at the population level in Chesapeake Bay varied with age structure.

The fact that age structure and ontogenetic diet shifts interact provides further justification for obtaining bluefish diet information by age or size. For example, the impact of the 1995 bluefish population on long-finned squid and butterfish was underestimated when pooled diet indices were used compared with diet indices that were partitioned by age or size (Fig. 5).

Comparison of biomass consumed by bluefish with that harvested by fisheries

Edwards and Bowman (1979) and Sissenwine et al. (1984) found that total piscivore consumption often exceeded fishery landings on Georges Bank. We have shown that bluefish alone consume an amount of squid and butterfish far exceeding the harvest of these species. How do our findings relate to the management of squid and butterfish? The current management plan for long-finned squid recommends a target yield of 21,000 t (Mid-Atlantic Fishery Management Council[5]). From calculations presented here bluefish consumed almost five times this amount of long-finned squid. Consistent with our findings, estimates of natural mortality for butterfish, long-finned squid, and boreal squid are high compared with other species (Anonymous, 1995; Atlantic butterfish, M=0.80; long-finned squid, monthly M=0.34; boreal squid, M>1.0). Our analysis does not allow us to determine what fraction of total prey mortality is due to bluefish consumption. Nor do we have estimates of impact of other predators on these prey. If we knew that bluefish were the dominant contributor to natural mortality in these prey, then questions regarding allocation could be dealt with more explicitly. For example, if the goal were to build larger squid stocks, would increased fishing mortality on bluefish be more or less effective than reductions in fishing mortality on squid? Future research should determine the magnitude of predation mortality resulting from bluefish and other predators. Until this information is available we must assume that predation mortality is similar to or below estimates of natural mortality for squid and butterfish. The management plan for these prey species assumes a high natural mortality (high predation mortality already taken into account) and fishing harvests are targeted accordingly.

However, these stock assessments assume that natural mortality is a fixed value. For prey of bluefish, this may not be true given the persistent changes in bluefish abundance on multiyear to decadal time scales. Natural mortality in squid and butterfish may vary greatly as a function of bluefish abundance. This has important management implications. For example, if bluefish abundance is high and remains so for extended periods and if this results in natural mortality rates on the prey that exceed the baseline natural mortality rates, then the biological reference points used in squid and butterfish management must be adjusted accordingly. Even if fishery removals are low in relation to those for other species, they may still contribute to population collapse by driving the prey population past the replacement level. Much more attention needs to be focused on assessment of the dynamics and predatory impact of bluefish if we wish to manage its prey, not to mention bluefish. Our results illustrate the importance of incorporating interspecific interactions in the management of marine fisheries (Sissenwine and Dann, 1991; Magnusson, 1995).

Bluefish may have limited influence on menhaden population dynamics because bluefish consumption of Atlantic menhaden was substantially below the fisheries landings of this species in our calculations. Oviatt (1977) estimated the aggregate demand for menhaden by bluefish in Narragansett Bay. She found that menhaden abundance was sufficient to meet the demands of bluefish even when the menhaden stock was low. Hartman and Brandt (1995b) found that combined predation by bluefish, weakfish, and striped bass on menhaden in Chesapeake Bay was low compared with fisheries harvest of menhaden.

There are several limitations to this analysis. The estimates of the biomass of prey consumed rely on several other estimated parameters. These include the VPA of bluefish biomass, the allometry of gross growth efficiency as a function of bluefish weight, diet estimates, and assumptions about the spatial and temporal location of the bluefish population. We therefore urge readers to view our estimates as rough approximations of the true values. At the very least, however, our analysis clearly suggests a need to greatly improve our knowledge of the population dynamics and foraging ecology of bluefish. In particular, more accurate data on bluefish abundance, spatial distribution, and diet as a function of bluefish size, season of the year, and habitat (e.g. estuary, coastal shoreline, or offshore) are required.

[5] Mid-Atlantic Fisheries Management Council. 1996. Amendment 6 to the fishery management plan and the draft environmental assessment for the Atlantic mackerel, squid, and butterfish fisheries. [Available from Mid-Atlantic Fishery Management Council, Room 2115, Federal Building, 300 South New Street, Dover, DE 19904-]6790, 16 p.]

For example, it has been shown that pooling bluefish diet by age or size class may over- or under-estimate the impact of bluefish compared with estimates of impact obtained when using age or size partitioned diets. Additionally, the diet of bluefish in estuaries (Oviatt, 1977; Hartman and Brandt, 1995c; Buckel et al., 1999a), where YOY bluefish are known to be dominant piscivores, was not considered here. Buckel et al. (1999a) showed that YOY bluefish in the Hudson River estuary are key predators on YOY striped bass and that recruitment success of striped bass is negatively correlated with YOY bluefish abundance. In the Chesapeake Bay, the percentage of menhaden in bluefish diet can be over 80% of the diet by weight (Hartman and Brandt, 1995c), much higher than the diet proportion we used in our analyses. A synoptic study examining the diet on the shelf and estuarine environments, as well as temporal and spatial distributions, will be required to determine the exact proportions of prey items in the coastal bluefish population.

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Sidescan-sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California

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Abstract.—The abundance and orientation of trawl marks was quantified over an extensive portion (>2700 km^2) of the Eureka, California, outer shelf and slope, an important commercial bottom trawling ground for such high-value species as rockfish, sole, and sablefish. Fishing logbook data indicate that the entire reporting area was trawled about one and a half times on an average annual basis and that some areas were trawled over three times annually. High-resolution sidescan-sonar images of the study area revealed deep gouges on the seafloor, caused by heavy steel trawl doors that act to weigh down and spread open the bottom trawls. These trawl marks are commonly oriented parallel to bathymetric contours and many could be traced for several kilometers. Trawl marks showed a quadratic relationship in relation to water depth, with the greatest number of trawl marks observed at ~400 m. There was a significant positive correlation between the number of trawl marks observed on the sidescan images and the number of annual trawl hours logged within reporting areas. This finding indicates that acoustic remote sensing is a promising independent approach to evaluate fishing effort on a scale consistent with commercial fishing activities. Bottom trawling gear is known to modify seafloor habitats by altering benthic habitat complexity and by removing or damaging infauna and sessile organisms. Identifying the extent of trawling in these areas may help determine the effects of this type of fishing gear on the benthos and develop indices of habitat disturbance caused by fishing activities.

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Fish. Bull. 97:786–801 (1999).

Concerns about trawl impacts on benthic fish habitats date back to the earliest use of this gear in the 13th and 14th centuries (de Groot, 1984), but the extent and longevity of these impacts have been difficult to quantify. The effects of trawling depend on the size and type of bottom trawl, footrope gear, bridles, doors, scope of main wires, trawling speed, duration, and repetition of trawling. Vulnerability of the sea floor to trawling impacts depends on the nature of the bottom type, benthic fauna, sedimentation rates, tidal velocity, and the degree of reworking of sediments caused by storms. Seabed disturbance can occur over the entire distance between the doors but is most pronounced in the region scoured by the trawl doors (Messieh et al., 1991), which have been shown to plough to depths greater than 15 cm (Caddy, 1973; Churchill, 1989).

In the short term, disturbance from bottom trawling can cause resuspension of sediments and make benthic infauna more available to scavenging predators (Kaiser and Spencer, 1994; Kaiser and Ramsay, 1997; Ramsay et al., 1997; Lindeboom and de Groot, 1998). Long-term shifts in abundance and

diversity of benthic fauna have been noted in areas where trawling has been conducted for extended periods of time (Reise, 1982; de Groot, 1984; Sainsbury, 1987; Hutchings, 1990; Collie et al., 1997; Lindeboom and de Groot, 1998). Chronic, long-term disturbance can delay or prevent recovery of ecological communities (Collie et al., 1997) and large-scale removal of macrobenthos can lead to permanent changes in the community (Jones, 1992; Collie, 1998; Rogers et al., 1998). The removal of benthic organisms and sedimentary structures (e.g. sand waves, depressions) by trawls can lead to modifications of the physical complexity of benthic habitats (Reise, 1982; Jones 1992; Auster et al., 1996; Collie, 1998; Dorsey and Pederson, 1998). Schwinghamer et al. (1996, 1998) found that trawling homogenized sediments on the Grand Banks of Newfoundland to a depth of at least 4.5 cm, thus reducing fine-scale complexity of the substrate. Sediment mixing and frequent bottom disturbance from trawling activity may affect resuspension fluxes and produce changes in the successional organization of soft-sediment infaunal communities (Pilskaln et al., 1998). Reduction or removal of benthic structural complexity can lead to reduced recruitment of benthic organisms and often to reduced production (Botsford et al., 1997).

The degree of impact on benthic habitat is related to the timing, severity, and frequency of disturbance (Watling and Norse, 1998). The average annual area swept by trawls on Georges Bank from 1976 to 1991 was between 200% and 400% of the total area (Auster et al., 1996). Trawling does not occur evenly over this area but is concentrated in locations that produce better catches and fewer obstructions to towing (Dorsey and Pederson, 1998; Auster and Langton, 1999). As a result, some areas are subjected to trawling at a much higher rate than these reported averages and other areas may not be trawled at all. The effects of dredging on tidal flats in the Wadden Sea persisted for more than 15 years (van der Veer et al., 1985); by contrast, experimental trawl marks in a relatively dynamic intertidal zone in the Bay of Fundy persisted only 2–7 months (Brylinsky et al., 1994). The effects of mobile fishing gear on biodiversity are most severe where natural disturbance is least prevalent, such as at outer continental shelf and slope habitats (Watling and Norse, 1998). An experimental program to examine the impacts of mobile fishing gear on the benthic ecosystems in Atlantic Canada clearly indicated that trawling changed the physical habitat structure on sandy bottom at 120–146 m over a three-year period (Gordon et al., 1998). Biomass of epibenthic organisms in the trawl catch decreased with repeated trawling and the total biomass, as sampled by epibenthic sled, was lower in trawled areas compared with adjacent habitats. Fishing effort is spatially nonuniform, and thus techniques are needed that will allow analysis of trawling activity, and thus trawling impacts, on spatial scales appropriate to the large scales on which fisheries operate. In this study, we examine sidescan-sonar records as one approach to this analysis.

The continental shelf off Eureka (water depths less than ~120 m) is relatively flat (<0.5 degree) and topographically very smooth due to large inputs of fine terrigenous sediments from the Eel and Mad Rivers and reworking by storms (Fig. 1; Goff et al., 1999). Bottom photographs and samples from the shelf generally show smooth, mud-covered bottom with small-scale bottom roughness resulting from bioturbation and occasional wave ripples (Wiberg et al., 1996). The dominant morphological feature of the shelf is the Eel River delta, a sediment bulge in water depths of 20 to 60 m adjacent to the mouth of the Eel River and elongated to the north. Slope deposits are dominated by fine-grain sediments that show a transition from sandy silt in the south near the Eel Canyon to clayey silt in the northern portion of the study area (Syvitski et al., 1996).

Seafloor depressions 5 to 20 m in diameter and several meters deep, termed "pock marks," are common on both the outer shelf and slope throughout the region. These depressions are inferred to form by the removal of particles during expulsion of gas and fluid from subsurface deposits (Yun et al., 1999). The excavation is thought to occur both at slow rates, inducing particle-by-particle removal, and at rapid rates during sudden release of subsurface gas by earthquake shaking or other mechanisms (Field and Jennings, 1987).

In addition to natural processes that modify the seafloor, such as bottom currents, landslides, and fluid-expulsion features, the sidescan data and bottom photographs also show evidence (trawl marks) of fishing activities that modify these benthic habitats. The northern California outer continental shelf and slope off Eureka are important commercial fishing grounds. The trawl fleet that fishes the area off Eureka presently consists of 36 vessels from Eureka and 29 from Crescent City.[1] These vessels range in size from 18 to 24 m (60 to 80 ft), the larger vessels having entered the fleet in recent years in response to a shift of fishing effort into deeper water. Trawl designs vary but currently the most common trawl configuration is a Nor'eastern design with 114-mm (4 1/2 in) diamond stretched-mesh polyethylene netting equipped with roller gear. Trawls are currently

[1] Quirollo, L. F. 1998. California Department of Fish and Game, 619 Second Street, Eureka, CA 95501. Personal commun.

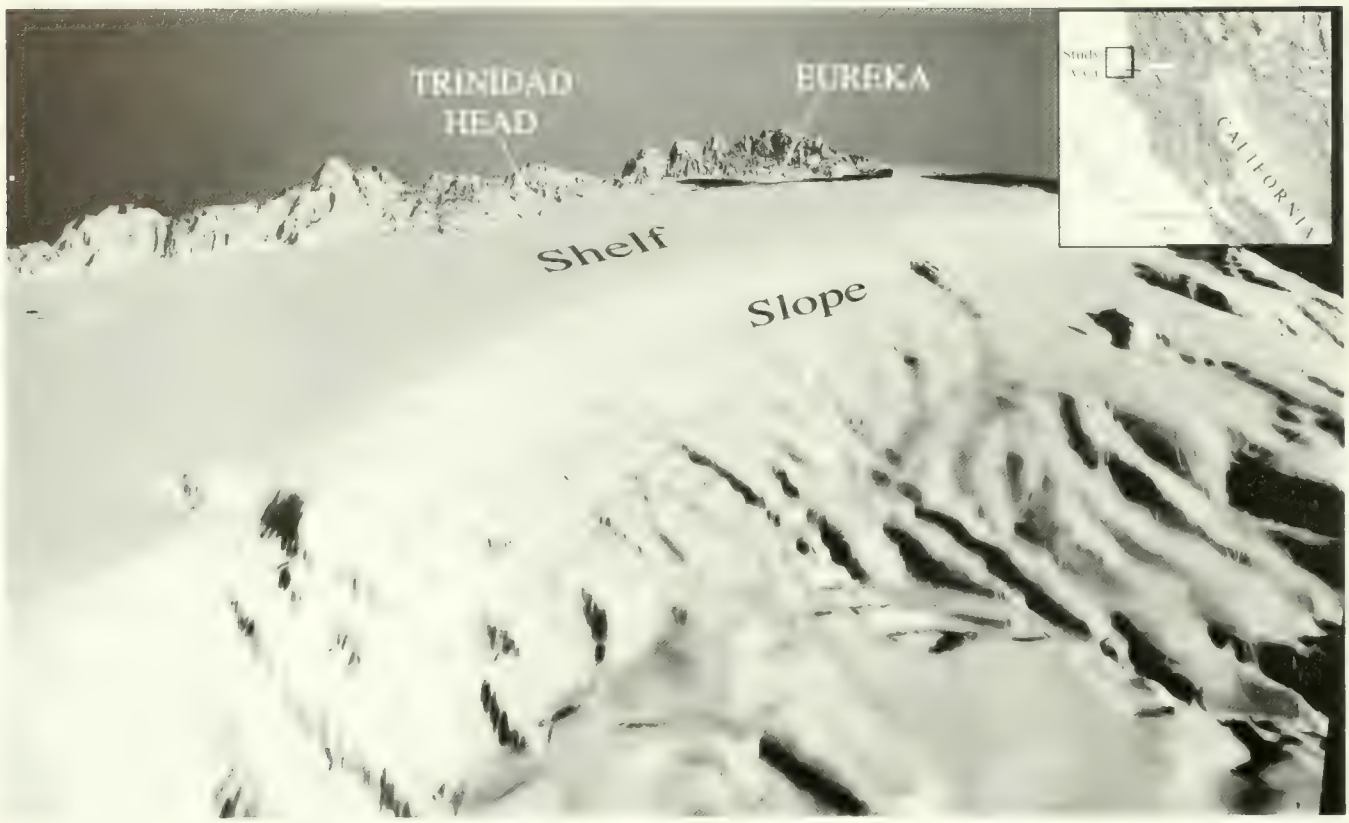

Figure 1

Perspective, shaded-relief view of the study area based on high-resolution multibeam bathymetry. Vertical exaggeration is 20×. The continental shelf (<120 m water depth) is bathymetrically smooth owing to large input of fine terrigenous sediments from the Eel and Mad Rivers and to reworking by storms. The southern portion of the shelf is dominated by the Humboldt slide. The northern portion of the slope is ~60 m deeper and ~7 km farther from shore than in the Humboldt slide area.

rigged with a 33.5-m (110-ft) net opening with trawl doors hung ~76–91 m (250–300 ft) apart.

The trawl fishery on the shelf primarily occurs over soft-sediment habitat and mainly targets flatfishes. The important species in this assemblage include English sole (*Pleuronectes vetulus*), Petrale sole (*Eopsetta jordani*), and sanddabs (*Citharichthys* spp.). The slope fishery occurs over rougher and more heterogeneous habitats that begin at the shelf break (~120 m) and continue to depths >900 m. The catch in this assemblage is dominated by Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), thornyheads (*Sebastolobus* spp.), and several rockfish species (*Sebastes* spp.). A midwater trawl fishery also exists in waters above the slope for Pacific whiting (*Merluccius productus*) and widow rockfish (*Sebastes entomelas*). The assemblages in this region are similar to those found along other portions of the U.S. west coast by the National Marine Fisheries Service triennial trawl surveys (Jay, 1996).

Groundfish are among the most diverse and economically valuable fishery resources along the west coast of the United States (NOAA, 1996). Diversity, quality, and extent of habitat are among the most important environmental determinants of distribution, abundance, and species diversity for groundfish (Carlson and Straty, 1981; Matthews and Richards, 1991). The broad spatial extent of these fisheries generally precludes careful examination of the nature of the exploited habitats, the relationship among species and habitats, and the degree to which fishing activities have affected these habitats. Conservation of fisheries habitat is an important consideration for sustaining fisheries production. The reauthorization of the Magnuson-Stevens Fisheries Conservation and Management Act requires incorporating the concept of "essential fish habitat" in Fishery Management Plans (Schmitten, 1996). Because fishing, particularly with bottom trawls, can alter essential fish habitat, it is important to quantify fishing activity and its effects on the associated habitat. The goals of this study are to evaluate the extent of marks from bottom trawls off Eureka, California, at a scale consistent with commercial fishing

activities and to compare these results with fishing-effort data from commercial fishery logbook data.

Materials and methods

Geological setting

The study area is the upper continental margin of northern California, north of Cape Mendocino. The shelf and slope in this region are within the Eel River Basin, a forearc basin filled with sediment derived from high sediment loads during the late Neogene (Clarke, 1992). The entire basin is highly faulted and folded from multiple episodes of deformation. Shearing and compression of the margin related to underthrusting of the Gorda plate beneath the North American plate has resulted in thrust faulting, uplift, and an overall youthful geologic setting, and this has produced varied relief and structure of the seafloor (Carver, 1987; Clarke and Field, 1989).

Studies of seafloor structure and sediment history of this area (Field et al., 1999; Gardner et al., 1999; Goff et al., 1999) have identified many features related to submarine landslides and to downslope sediment transport through channels and gulleys. Sidescan-sonar images of the seafloor along the shelf and slope, as well as multibeam maps, high-resolution seismic reflection data, and instrumented tripods from complementary investigations, all show abundant evidence of modern processes at work on the seafloor (Field and Jennings, 1987; Alexander and Simoneau, 1999; Field et al., 1999; Gardner et al., 1999; Goff et al., 1999; Yun et al., 1999).

There are three main types of relief on the seafloor in this region. Along the slope, in the center of the study area, a large growth fold (anticline) has uplifted through the modern seafloor, exhibiting 100 m of steep relief. South of the anticline, the slope between 120 and 600 m depths is dominated by the Humboldt slide, an area where slope deposits have undergone deformation and limited downslope movement (Field and Barber, 1993; Gardner et al., 1999). North of the anticline, the slope is crossed by a series of shallow gullies that are 100 to 200 m wide and 1 to 2 m deep (Field et al., 1999). Gullies are spaced about 200 to 300 m apart. Gullies also occur south of the anticline where they are generally fewer in number and somewhat deeper (~20 m). The gullies are thought to represent sediment pathways during earlier periods when sea level was at a lower position.

Sidescan survey

Through a collaborative effort of the U.S. Geological Survey (USGS) and the National Marine Fisheries Service (NMFS), we examined sidescan-sonar data off Eureka, California, collected by the USGS during the STRATA FORMation on Margins (STRATAFORM) program sponsored by the Office of Naval Research (Nittrouer and Kravitz, 1996; Nittrouer, 1999). A grid of 1600 line kilometers of high-resolution, digital, deep-towed (95 kHz) sidescan-sonar data was obtained during 1995 and 1996 (Fig. 2). The sidescan-sonar images were obtained by using the USGS Datasonics SIS-1000 chirp sonar system and an ISIS data-acquisition system. The sidescan sonar operates as a swept FM signal with a frequency band from 90 to 110 kHz (port channel sweeps from low to high, starboard channel sweeps high to low). Usual swath width during the cruises was 0.5 s (750-m swath). Sidescan data were recorded on magneto-optical disks and downloaded to a DEC ALPHA workstation. The digital sidescan-sonar data were all processed with USGS MIPS image-processing software (Chavez, 1984; 1986). The raw data were geometrically corrected (slant range) by using the position, heading, speed, and nadir depth of the ship. Each of the 8-bit image pixels was geometrically located by assuming a flat seafloor which introduces a certain amount of uncertainty into the actual location of any given pixel. Our estimated location accuracy was about 100 m. After the geometric corrections were made, anamorphic corrections were applied to account for the aspect ratio between along- and across-track directions. Radiometric corrections had to be applied to the 8-bit digital number (DN) that represents backscatter. Each sidescan line was subdivided into segments and, for each segment, the average DN for each binned range was normalized to the mean of all the binned ranges within that segment. Each segment was several hours long, and this correction produced tone-matched adjacent segments.

Trawl marks

Trawl marks appear on the sidescan sonographs as long, narrow, linear depressions (Fig. 3). Trawl marks were traced on mylar overlaid on the sidescan records. Each sidescan track line was divided into 10-min time intervals. Vessel speeds during the surveys varied between 3 and 4 knots, and therefore each 10-minute interval covered from 0.9 to 1.2 km along the ship's course. The sidescan record covered a 750-m swath so that 10-min segments represent from 675,000 m^2 to 900,000 m^2 of area. To quantify the number of trawl marks per time interval, lines were drawn perpendicular to the course of the sidescan track line, and trawl marks that bisected these lines were counted. Mean trawl mark length was 0.77 km (SD=0.26) for 20 randomly selected 10-min

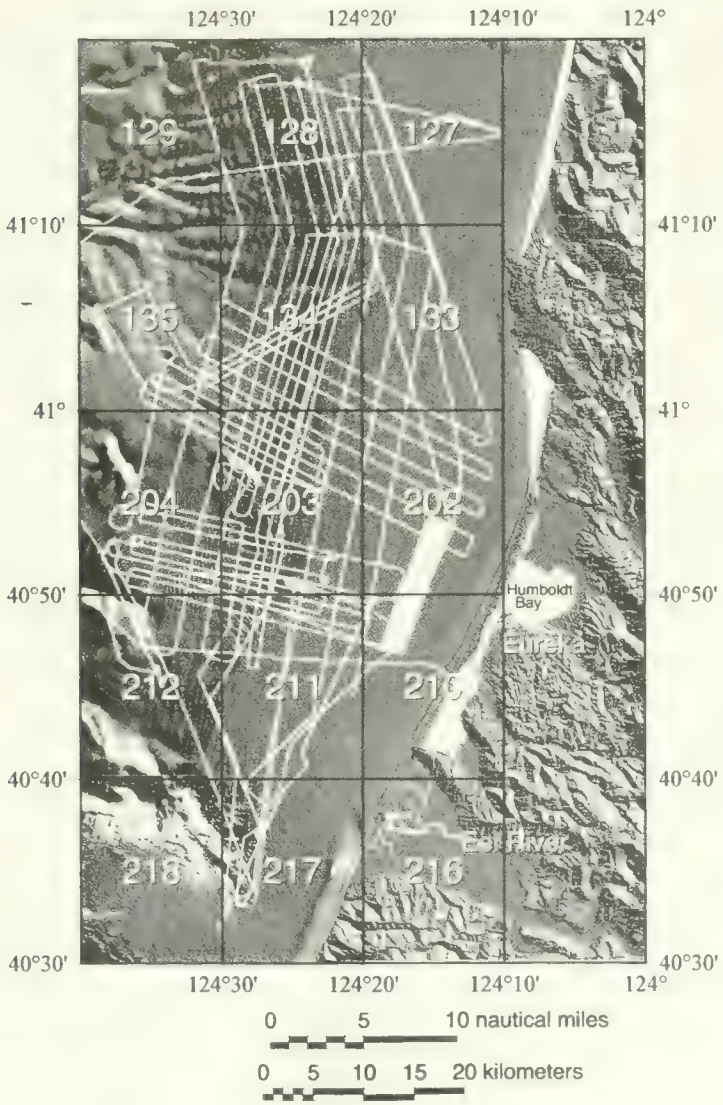

Figure 2

Track lines for high-resolution sidescan-sonar surveys. The reporting blocks from California Department of Fish and Game that are used for logbook data entry are superimposed on the survey area. Blocks are 10 minutes of longitude and 10 minutes of latitude on a side with block number in the center.

intervals from 10 different sidescan track lines (Fig. 4). From these results, it was determined that two random perpendicular lines were needed to properly sample each 10-min interval and minimize double-counting of trawl marks. Using a sample of 50 randomly selected 10-min time intervals from 10 sidescan track lines, we counted the actual number of trawl marks and compared this number with the mean number counted with the perpendicular line intercept method described above. The mean proportion of trawl marks counted with this sampling method to actual number of marks was 0.84 (SD=0.11). Trawl mark density in km^2 was calculated from each time interval and incorporated into a Geographical Information System (GIS) for analysis and contouring.

The angle of each trawl mark was measured in relation to the two perpendicular lines used to quantify trawl marks in all 10-min intervals. These angles were adjusted for the course of the sidescan track and computed in relation to magnetic north. Mean angles for each time interval were then calculated and plotted on a polar plot in an $r = f(\theta)$ format, where r is the number of trawl marks and theta (θ) is the angle relative to 0°. The grand mean angle and 95% CI were computed with the mean values from each time interval (Zar, 1984).

Fishing effort

Trawlers provide information on catch and effort of individual trawl hauls to the California Department of Fish and Game (CDF&G). Hauls are spatially recorded in blocks that are 10 minutes of latitude by 10 minutes of longitude (Fig. 2). Blocks within the Eureka STRATAFORM survey area were extracted from the NMFS Tiburon Laboratory groundfish database and used in these analyses. Trawling is prohibited by state law within 5.6 km (3 nm) of the coast. All reporting blocks adjacent to the coast were truncated for all estimates and comparisons.

Pacific whiting form extensive midwater aggregations during the day, and the fishery is conducted almost exclusively with midwater trawls (Dorn and Saunders, 1997). Because fishermen did not report whether their trawl hauls were bottom trawls or midwater trawls, all trawl hauls with catches of Pacific whiting greater than 454 kg (~1000 lb) were eliminated from these analyses. Mean annual fishing effort (trawl hours) was calculated for each reporting block within the Eureka area for the years 1990 to 1994. Depths from the logbook data were used to obtain mean fishing depths for each reporting block for comparisons with fishing effort.

The reporting block grid was incorporated into a GIS and the mean density of trawl marks was calculated for each block (Table 1). Water depths from a high-resolution multibeam mapping survey (Goff et al., 1999) were binned to obtain mean bottom depth in each block for comparison with mean number of trawl marks. Effort, expressed as mean annual trawl

hours per block, was compared to the mean number of trawl marks in each reporting block with a Spearman rank order correlation. Two reporting blocks (129 and 218) were excluded from this analysis owing to a lack of adequate sidescan coverage. To estimate the total area swept by bottom trawls on an annual basis, the total annual number of fishing hours per reporting block was multiplied by a typical vessel speed (5.5 km/h) and a typical door to door width of 85 m.

Detrended correspondence analysis (DCA) was used to identify clusters of similar reporting blocks in ordination space on the basis of fish assemblage structure from CDF&G logbook data (Ludwig and Reynolds, 1988). A matrix of reporting blocks by catch was created for use in this analysis. Habitat types were defined *a priori* by depth and physical characteristics of the habitat from previous geological surveys and then overlaid on the station clusters created by DCA. A Kruskal-Wallis rank sum test (Hollander and Wolfe, 1973) was used to compare the density of trawl marks and total fishing hours per reporting block in each habitat type discerned by DCA. Pairwise comparisons of trawl marks and fishing effort between habitats was conducted by using Dunn's multiple comparison procedure at $\alpha = 0.05$ (Hollander and Wolfe, 1973).

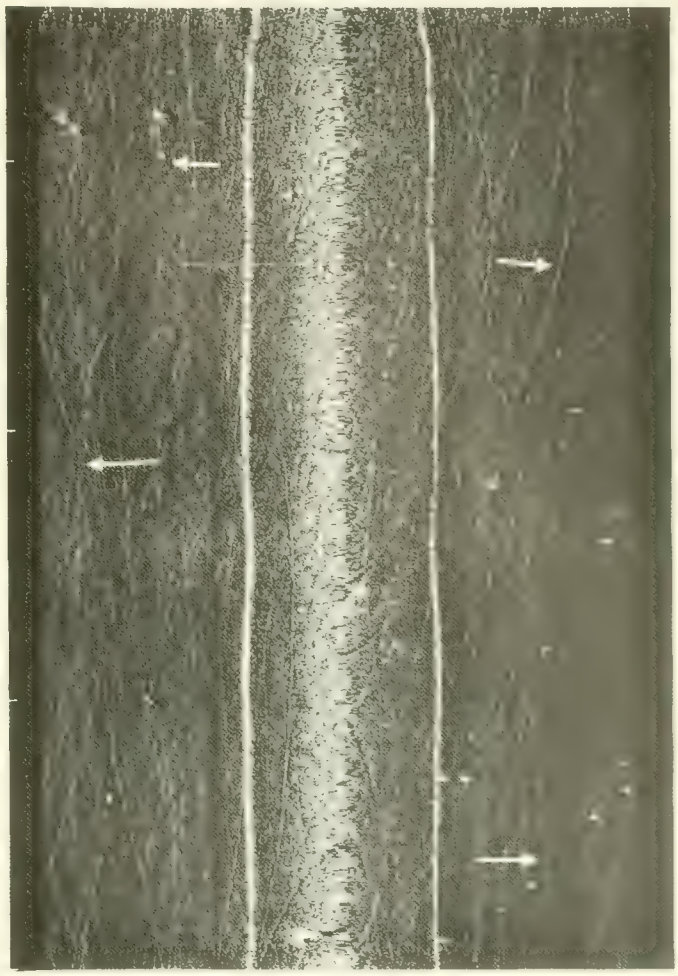

Figure 3

Sidescan-sonar image (white is shadow; dark is reflection) of trawl marks on the seafloor at a water depth of ~150 m. Sidescan swath width is 750 m. Tick marks are 5-min time intervals (~0.55 km). Arrows point to examples of trawl marks. Shallow circular depressions on the sonograph are gas pockmarks. Ship's course for this sonogram is 345°.

Results

We measured the range, density, and orientation of marks on the seafloor caused by trawling activity as resolved by the sidescan-sonar records. Of the 1246 10-min intervals examined, ~10% were washed out and could not be analyzed. Densities of trawl marks/km^2 per 10-min interval ranged from 0.00 to 98.55 and mean density per block ranged from 0.94 to 38.3 with a grand mean of 20.0 marks/km^2 (Table 1). Trawl marks were most abundant on the slope, particularly the northern portion and least abundant on the continental shelf (Fig. 5).

Trawl marks commonly were oriented parallel to isobaths and some could be traced for several km (Fig. 6). The overall mean trawl direction was 352.6° (95% CI +/–5°) (Fig. 7) which agrees with the general orientation of isobaths in this area. Because trawl marks were generally orientated in the north–south direction along isobaths, sidescan tracks orientated in the east–west direction (>45° and <135°) might not distinguish as many trawl marks in relation to those orientated in the north–south direction. Using 25 randomly selected time intervals from five east-west sidescan track lines and 25 from five north–south track lines, we found that the proportion of trawl marks sampled with the perpendicular line intercept method was not significantly different from the actual number of trawl marks for the two track line orientations (Mann-Whitney rank sum test=759.5, P=0.775).

We compared the orientation of trawl mark angles between east–west and north–south orientations by selecting seven locations where east–west and north–south sidescan-sonar track lines intersected during the 1996 survey. The intersecting time interval, along

with one time interval to either side were pooled for each orientation (21 time intervals for each orientation) and compared by using a Watson-Williams two-sample test for mean angles (Zar, 1984). There was a significant difference (F=44.7, P<0.001) in the mean angle of trawl marks detected along north–south orientated track lines (mean=357.9) compared with east–west orientated track lines (mean=294.5) at these intersection points.

The mean density of trawl marks in each CDF&G reporting block fitted a quadratic relationship with water depth ($y=-0.0002x^2 + 0.1374x + 2.9353$, R^2=0.501, P=0.04). The lowest density of trawl marks was observed in the shallowest water with maximum number of trawl marks observed at ~400m depth (Fig. 8). Mean annual trawl hours (1990–94) also fitted a quadratic model with water depth for each reporting block ($y=-0.0082x^2 + 8.7015x - 960.57$, R^2=0.723, P<0.001) (Fig. 8). There was a significant positive correlation between the density of trawl marks and the mean annual number of trawl hours per reporting block (r_s=0.573, P=0.048).

The fishing blocks off Eureka can be separated into three depth zones on the basis of fish assemblages analyzed by DCA (Fig. 9). The upper and mid slope blocks are relatively close in DCA ordination space, whereas the shelf blocks showed a distinct assemblage structure. The shelf blocks nearest the coastline have effective fishing depths of ≤102 m (Table 2). From logbook data, the dominant species at these depths are flatfishes (e.g. sanddabs, Petrale sole, and English sole) and rockfishes. Dominant species from trawling on the upper slope (175 to 437 m) primarily consisted of Dover sole and rockfishes. Thornyheads, Dover sole, and sablefish are the dominant species on the mid slope (effective fishing depth from ~595 to 837 m).

The mean density of trawl marks was significantly different (Kruskal-Wallis H=287.4, P<0.001) among the three depth zones recognized by DCA (Fig. 10A). Upper and mid slope depths were not significantly different from one another (P>0.05) but both had significantly greater numbers of observable trawl marks than the shelf depth zone (P<0.05). Mean annual fishing effort per block also showed significant differences among depths (Kruskal-Wallis H=9.5, P=0.009, Fig. 10B). Fishing effort was lowest in the shelf habitat and highest in the upper slope, although the upper slope and deep slope depth zones were not significantly different from one another (P>0.05).

The cumulative annual area swept by commercial bottom trawls, as calculated from logbook data, was compared to the total area in each reporting block (Fig. 11). The entire study area was trawled ~1.5 times on an average annual basis. The area trawled exceeded the total block area in the majority of the blocks. This

Table 1

Summary statistics for density estimates of trawl marks in each California Department of Fish and Game (CDF&G) reporting block. Block numbers with asterisks are excluded from comparative analysis with fishing effort owing to small sample size and lack of adequate block coverage.

CDF&G block	Mean (no/km^2)	SD (no/km^2)	Max (no/km^2)	Min (no/km^2)	n
127	25.22	16.77	52.92	0.00	34
128	35.07	18.56	98.55	2.09	132
129*	31.19	7.94	45.08	21.59	13
133	11.80	13.20	49.13	0.00	81
134	38.26	11.82	63.49	0.00	144
135	22.02	10.69	52.11	1.39	34
202	4.13	6.44	26.67	0.00	169
203	18.01	12.65	43.87	0.00	159
204	22.82	15.71	64.09	0.00	115
210	0.94	2.25	14.03	0.00	69
211	10.99	16.89	76.75	0.00	102
212	28.98	13.56	66.42	8.25	39
217	27.39	27.23	75.55	0.00	25
218*	28.68	15.58	39.69	17.66	2
Mean	19.99	18.34	98.55	0.00	Σ = 1118

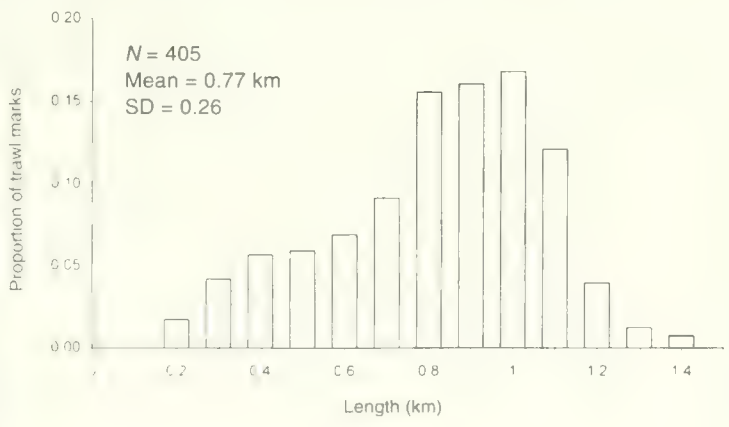

Figure 4

Frequency distribution of trawl-mark length per 10-min interval. Ten minute time intervals ranged from 0.77 to 1.2 km in length (mean=0.91). Data are from 20 randomly selected 10-min intervals from 10 different sidescan tracks.

was particularly true in the deeper blocks where the ratio of area trawled to block areas ranged from 127% to 339%.

The mean trawl depth and mean duration of hauls for bottom trawls off Eureka has increased steadily since the early 1980s (Fig. 12A). Along with this change in fishing depth has come a shift in the composition of species landed. Thornyheads are deeper-water species and their catch contribution has increased from ~4% of the total catch in the late 1970s to ~14% in the 1990s. Conversely, the English sole is a shallow-water flatfish whose landings have declined from nearly 7% of the total catch in the late 1970s to 2–3% in the 1990s.

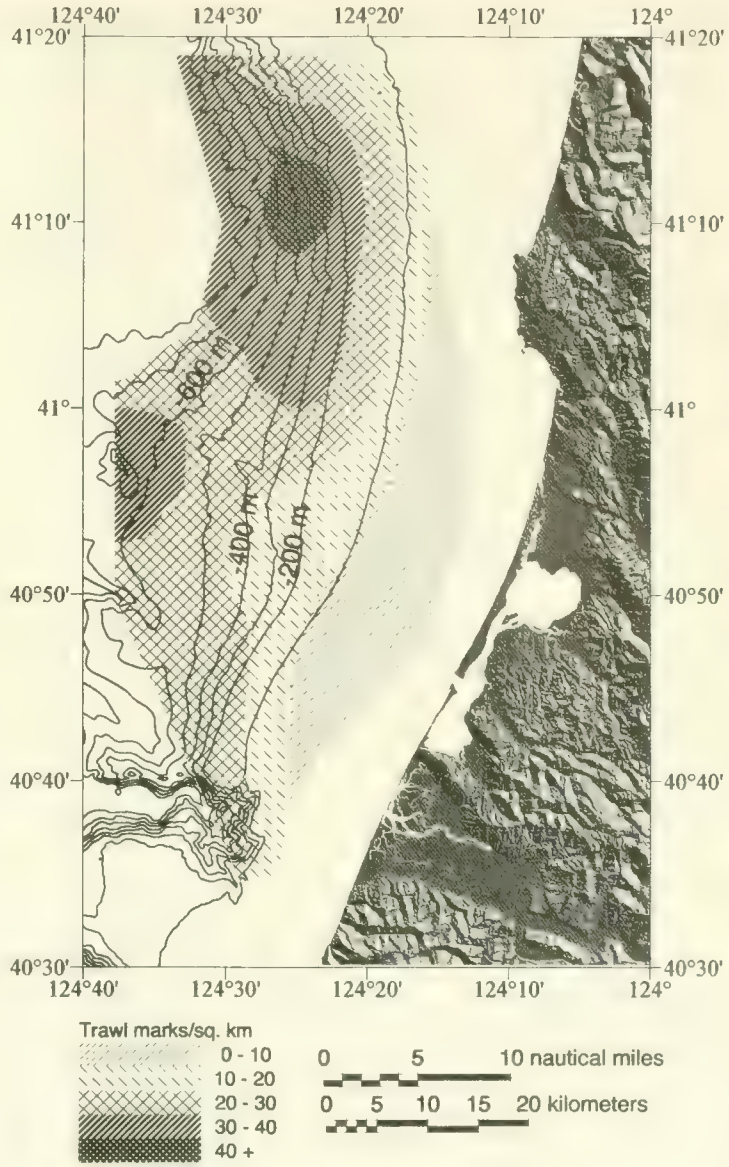

Figure 5

Contour plot of trawl mark densities (number/km^2) derived from 10-minute intervals along sidescan survey track lines. Actual locations of data points are in Fig. 6.

Discussion

Utility of sidescan sonar

Acoustics are useful in fisheries for stock assessment (Karp, 1990), for remotely sensing characteristics of bottom habitat (Able et al., 1987; Greenstreet et al., 1997; Mayer et al., 1997; Yoklavich et al., 1997; Auster et al., 1998a, 1998b), and for assessing impacts to fisheries habitat (Auster et al., 1996; Collie et al., 1997). Our results demonstrate that the use of acoustic remote sensing also presents a promising independent approach for evaluating fishing effort on a spatial scale consistent with commercial fishing activities. Sidescan-sonar data are useful for identifying the location of trawling activity, as well as for evaluating the amount of disturbance to the seabed, and may be used in developing indices of habitat disturbance caused by fishing activities. Despite minimal sidescan coverage in some reporting blocks and biases in the logbook data associated with misreporting, there was a significant positive correlation between the density of trawl marks per reporting block from sidescan-sonar data and the mean annual number of trawl hours. A quadratic relationship with depth was observed for the number of trawl marks and fishing effort per reporting block with maximum values at ~400 m and ~500 m, respectively. This relationship, together with the density contour plot of trawl marks and the vector plot of trawl orientation, shows that fishing effort was concentrated on the upper to mid slope and along bathymetric contours.

The entire study area off Eureka is trawled ~1.5 times its total area on an annual basis. Because of narrow bands of rocky outcrops and anticlines, trawlable fishing area within the mid slope reporting blocks is less than the total area of the blocks. The area swept by trawls is therefore an under-estimate of the effective fishing area that is impacted by trawl gear in these blocks. Gislason (1994) estimated that trawling swept the entire area of the North Sea annually, with some fishing grounds in the southern North Sea likely being swept more than three times a year by beam trawls. This type of chronic impact on the seafloor can have a long-term effect on the local benthic epifauna (Rogers et al., 1998). For example, there is abundant evidence of rich ecological communities associated with cold-seeps and exten-

sive bioturbation off Eureka (Syvitski et al., 1996). Released gases and fluids from cold seeps are rich in methane and sulfide and support unique productive cold-seep biological communities (Syvitski et al., 1996). The magnitude of trawling activity in this area has the potential to modify these communities by direct physical damage or by smothering from resuspended sedimention.

There has been increased interest in recent years on the impacts of fisheries on the marine environment (Dayton et al., 1995; Boehlert, 1996; Lindeboom and de Groot, 1998; Watling and Norse, 1998), and an important component is the relationship between exploited fish species and their associated habitats (Schmitten, 1996). With a greater understanding of these associations, concerns have been raised about the adverse impacts that mobile fishing gear may have on the entire ecosystem. The severity and duration of disturbance are both factors that affect ecological communities (Gislason, 1994; Connell et al., 1997; Tuck et al, 1998; Auster and Langton, 1999). Mobile fishing gear, such as trawls, is the most widespread form of direct disturbance to marine systems below depths affected by storms (Watling and Norse, 1998). Natural disturbances to the benthic community off Eureka probably occur from high-energy wave events, floods, and even tectonic activity. The first two processes likely have a greater impact in the shallower water on the shelf, and the latter process is likely too infrequent to play a major role in impacting the benthos. Thus, in the habitat covered by this study, trawls represent the greatest form of direct disturbance to the benthic habitat—a finding that is consistent with the conclusions of Watling and Norse (1998) for depths below the influence of storms. The extent and location of fishing activity, noted in this study from logbook data and sidescan-sonar records, can potentially have a large impact on the local ecological communities, particularly on the slope where the frequency and magnitude of natural disturbance is less than that on the shelf.

Figure 6

Vector plot showing orientation and magnitude of trawl marks along sidescan track lines. Length of arrow is proportional to the density of trawl marks in each 10-min interval, and direction is the mean angle of all trawl marks in each time interval. Note that angles are plotted in relation to north so that trawls towed north or south resulted in the same orientation.

Examination of trawl marks was not the primary goal of the sidescan-sonar survey conducted off Eureka (Syvitski et al., 1996). Consequently, there are aspects of the survey method that could have been conducted differently to improve the quality of these data. Because fishing activities in this area are generally conducted along the north–south bathymetric contours, sidescan-sonar tracks oriented east–west tended to resolve slightly fewer trawl marks. Any future study of trawl marks using sidescan sonar should concentrate tracks to orientations subparalleling trawling directions in order to maximize the resolution of the survey.

There are biases associated with this method, particularly in a dynamic physical location like the northern California continental margin. Estimates of the actual number of trawl marks are minimal because of variability in resolution of the sidescan records, obliteration of older trawl marks by more recent trawling, burial by sedimentation or reworking of the seafloor by

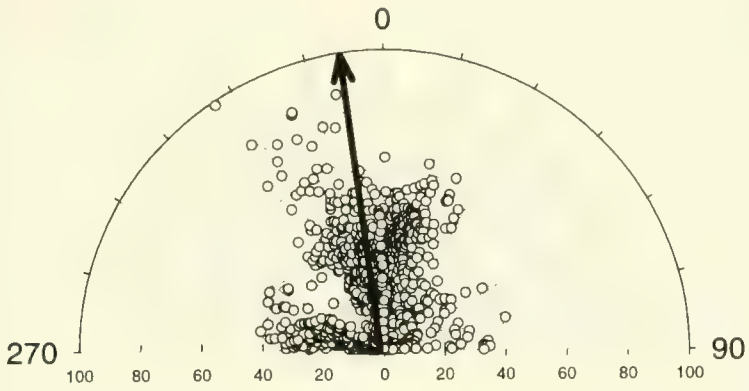

Figure 7

Polar plot of mean angle and density of trawl marks for each time interval. Polar plot in an $r = f(\theta)$ format where r is the density of trawl marks and theta (θ) is the angle relative to 0°. The grand mean trawl direction was 352.6° (95% CI +/–5°).

large waves, particularly at shallower depths. Trawl marks may persist for longer duration in deeper water where sedimentation rates are lower and storm waves have a lessened or negligible effect. Shelf sediment presently accumulates 2 to 10 times faster on the shelf than on the slope (1–3 mm/yr on the slope; 6–10 mm/yr on the shelf based on ^{210}PB activities; Alexander and Simoneau, 1999; Sommerfield and Nittrouer, 1999). At present rates, and assuming trawl track depths of ~15 cm, it would take 50–75 years to fill in a typical trawl mark, but evidence shows that small natural gullies on the slope are being draped and are infilled at present and thus maintain their shape and relief even though they are in the process of being buried (Field et al., 1999). The sedimentation rates on the shelf are higher than on the slope (the flood deposits from the 1964 Eel River flood now lies ~45 cm below the seafloor) (Sommerfield and Nittrouer, 1999), and annual storm waves resuspend sediments at depths up to 100 m. Resuspension and redeposition of silt particles may lead to draping of trawl gouges and thus preserve their shape and relief on the seafloor. In the presence of bottom currents, which usually are present from tides, storm waves, or boundary flows, the resuspended particles may fill in the trawl gouges and thus slowly erase them over time. Since fishing effort in the study area was shown to be concentrated in water deeper than 100 m, these effects are possibly compounded by the longevity of trawl marks in this habitat. Research is needed to address the longevity of trawl marks in various environments as well as to determine the impacts on (and recovery of) diversity and production in benthic communities.

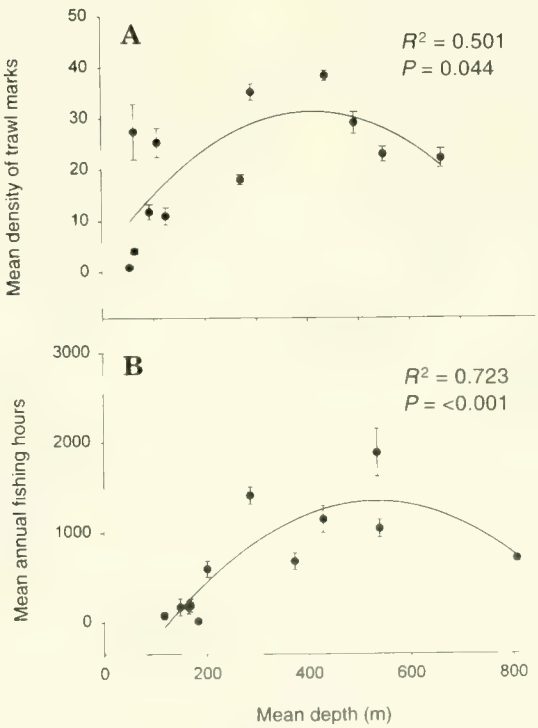

Figure 8

(**A**) The nonlinear relationship between mean density of trawl marks per 10-min interval by CDF&G reporting block depth (m). Mean trawl mark block depth is calculated from the mean depth of 10-min intervals along the sidescan track in each reporting block. (**B**) Mean annual fishing hours per reporting block and block depth (m). Mean fishing hour block depth is calculated from the depths reported from logbooks in each reporting block. Error bars are standard error of the mean.

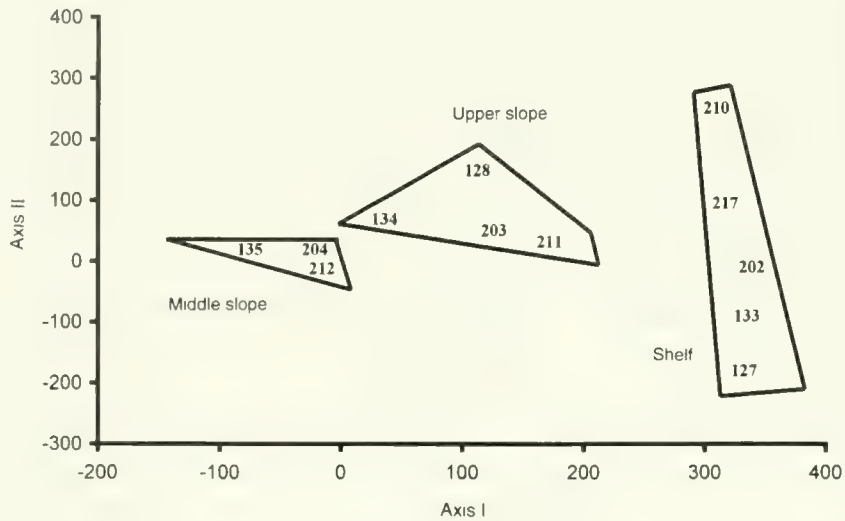

Figure 9

Results of a detrended correspondence analysis of mean annual species catch composition (1990–94) in CDF&G reporting blocks off Eureka. Three clusters are recognized as unique depth zones. Numbers are CDF&G reporting block numbers.

Table 2

Characteristics of California Department of Fish and Game (CDF&G) reporting blocks by habitat zone. Values for fishing depth are mean depth per trawl in each reporting block from logbook data (1990–94). Block depth and area are calculated from Geographical Information System (GIS) data and exclude areas within the 5.6-km (3-nmi) no trawl zone. Values for dominant species are percentages of mean total annual catch (1990–94).

Habitat zone	Block	Fishing depth (m)	Block depth (m)	Block area (km^2)	Fishing effort	Dominant species caught					
Shelf											
	127	68	83	251	191	Sanddab	30.31	English sole	27.59	Petrale sole	14.82
	133	102	83	207	16	Sanddab	33.31	English sole	14.35	Widow rockfish	9.87
	202	67	69	202	169	Sanddab	48.46	English sole	12.80	Petrale sole	11.88
	210	93	52	55	78	Rockfish	29.46	Sanddab	25.85	Petrale sole	14.25
	217	101	96	147	170	Widow rockfish	52.36	Rockfish	12.64	Sanddab	11.29
Zone mean		86	77	$\Sigma = 862$	$\Sigma = 623$	Sanddab	29.84	Rockfish	13.80	English sole	13.15
Upper slope											
	128	359	347	259	691	Dover sole	40.10	Rockfish	22.78	Sablefish	13.92
	134	437	425	259	1156	Dover sole	60.50	Sablefish	16.48	Thornyhead	7.76
	203	265	260	260	1425	Dover sole	34.07	Rockfish	21.41	Petrale sole	10.29
	211	175	118	256	599	Dover sole	22.68	Rockfish	22.52	Sanddab	13.49
Zone mean		309	288	$\Sigma = 1034$	$\Sigma = 3871$	Dover sole	39.34	Rockfish	10.18	Sablefish	10.95
Mid slope											
	135	837	873	259	707	Thornyhead	45.75	Dover sole	33.11	Sablefish	16.21
	204	539	583	260	1054	Dover sole	57.06	Sablefish	15.45	Thornyhead	12.13
	212	525	570	260	1900	Dover sole	51.92	Thornyhead	16.80	Sablefish	15.63
Zone mean		634	675	$\Sigma = 779$	$\Sigma = 3661$	Dover sole	47.36	Thornyhead	24.89	Sablefish	15.76

The general temporal trend in fisheries development begins with localized fisheries that then expand geographically and to less accessible habitats, such as the deep sea (Deimling and Liss, 1994). In the present study, mean trawl depths have increased over the years as a result of changes in management strategies, changes in market demands, and overfishing of nearshore resources. Shortspine thornyheads (*Sebastolobus alascanus*) and longspine thornyheads (*S. altivelis*) are slope rockfish species whose landings have increased along the West Coast in recent years (Ianelli et al., 1994) whereas English sole has decreased. An export market for thornyheads developed during the 1980s because a similar and highly valued species (*S. macrochir*) was depleted off Japan (Rogers et al., 1997). As the Japanese market developed, the trawl fishery moved into deeper water following a typical pattern (Deimling and Liss, 1994) where longspine thornyheads and larger shortspine thornyheads are most common. Several of the most important species in the trawl catch (e.g. Dover sole and sablefish) segregate at depth by sex, size, and maturity stage. These biological characteristics as well as size and harvest restrictions makes interpretation of changes in the catch of these species difficult to interpret.

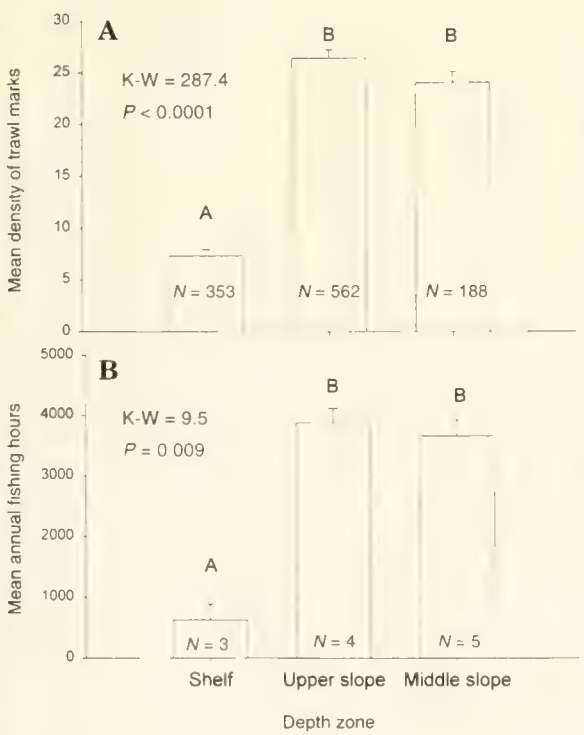

Figure 10

(**A**) Mean density of trawl marks per 10-min interval for the three habitat zones recognized by DCA. N = the number of time intervals in each habitat zone. (**B**) Mean annual fishing hours per CDF&G reporting block for the three habitat zones recognized by DCA. N = the number of reporting blocks in each habitat zone. Error bars are standard error of the mean. Statistical results from Kruskal-Wallis rank sum test. Dunn's multiple comparison procedure, $\alpha = 0.05$. Habitats with the same letter designation are not significantly different from one another.

Implications for management

The groundfish trawl fishery has experienced declining catches and increasing regulation in recent years. Current management strategies are imposed primarily on individual species or among small groups of congeneric species. These strategies do not address the impact to essential fish habitat from fishing activities and therefore may not be appropriate for the long-term sustainability of these resources. Marine reserves or harvest refugia are an effective management strategy that can help protect and maintain the complexity and quality of fish habitat as well as mitigate the direct effects of fishing (Bohnsack, 1996; Bohnsack and Ault, 1996; Auster and Shackell, 1997; Yoklavich, 1998). A number of studies have noted reduced diversity and abundance of emergent epifauna in trawled areas compared with adjacent areas closed to fishing (Bradstock and Gordon, 1983; Auster et al., 1996). The demersal trawl fishery off northwest Australia was thought to be responsible for a significant loss of emergent epifauna and decreased fish productivity (Sainsbury, 1987, 1988), both of which recovered in an area closed to fishing. The establishment of harvest refugia may be the most effective method of reducing the impact of trawls to benthic habitat and subsequently may help to improve the sustainability of the associated fish assemblages.

Detailed analysis of sidescan-sonar data has allowed us to map and quantify trawl marks in relation to fishery and habitat distributions. The combination of geophysical data with fisheries dependent and independent data in a GIS provides the ability to examine the impact of trawling at a scale appropriate for fisheries management. Evaluation of benthic habitat disturbance caused by fishing activities is important for meeting the mandate of the Sustainable Fisheries Act. Developing indices of benthic habitat disturbance can be valuable in comparing the impact of fishing activities among different areas and in establishing baselines for evaluating future management strategies such as closed areas.

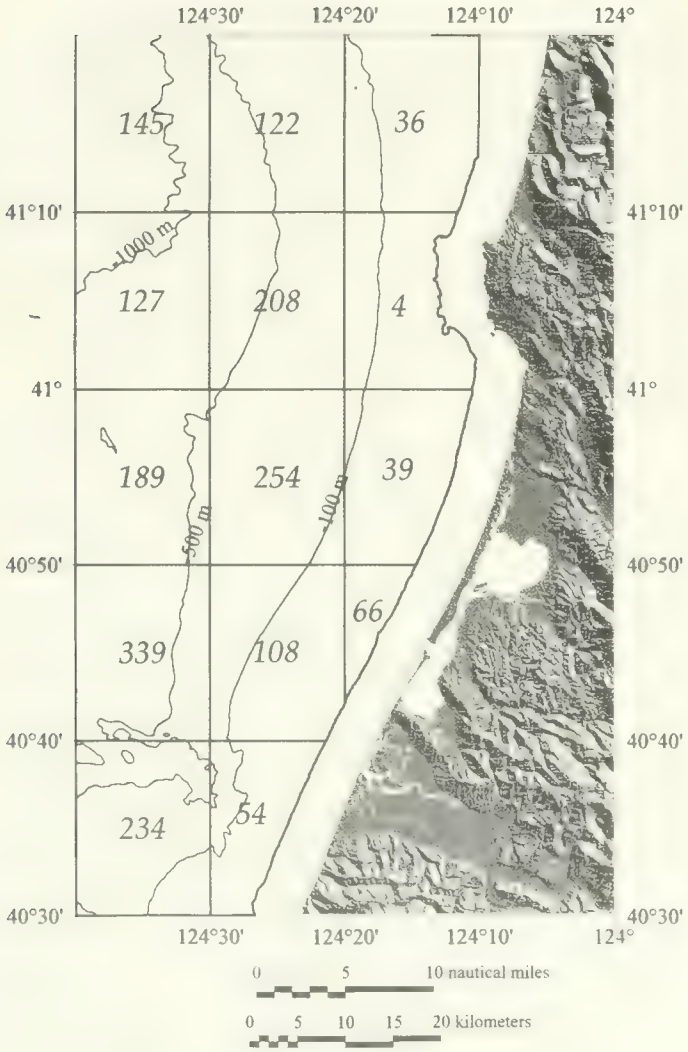

Figure 11

Total area trawled within each reporting block as a percentage of the total block area. Area trawled was calculated from the product of mean annual fishing effort (1990–94) from logbook data, typical vessel speed (5.5 km/h), and a typical trawl door to trawl door width of 85 m. "No trawl" areas within 5.6 km (3 nmi) of shore are not included in the total area calculations.

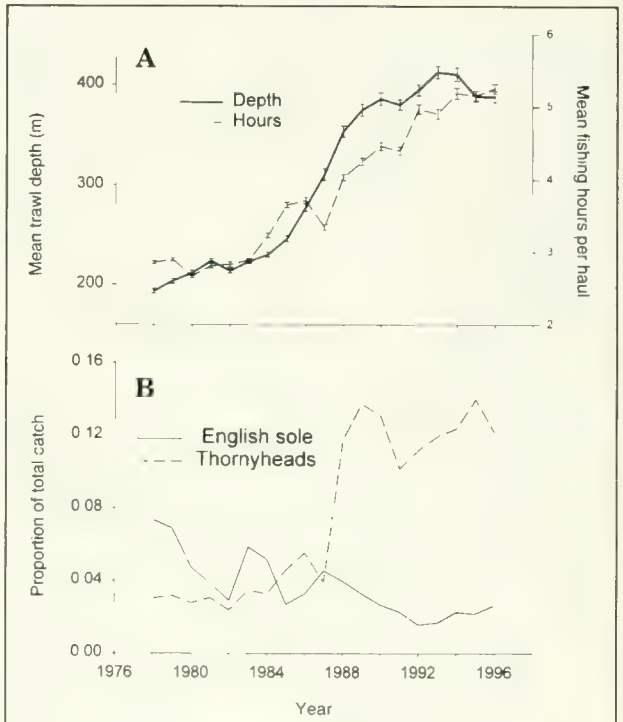

Figure 12

(**A**) Mean annual trawl depth and mean fishing hours per trawl haul off Eureka from 1978 to 1992. Error bars are standard error of the mean. (**B**) Proportion of total groundfish trawl catch of thornyheads and English sole from 1978 to 1994.

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Reproductive versus somatic tissue growth during the life cycle of the cuttlefish *Sepia pharaonis* Ehrenberg, 1831

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Abstract.—The effect of maturation on relative growth of somatic tissues was investigated by measuring and comparing monthly changes in dry weight of somatic tissues and reproductive organs. In both sexes, reproductive tissues grew in relation to total body mass; at maturity female reproductive tissue was 16% of total dry body mass, whereas male reproductive tissue was 2.6%. In females, the relative mass of the mantle and head decreased during maturation, whereas the relative mass of the viscera increased. In males, the mass of the viscera increased with maturation, but no decreases occurred. The percentage composition of protein in the mantle and head of females for each maturity stage did not differ significantly. For both sexes, the digestive gland mass remained relatively constant throughout the different maturity stages and seasons, and analysis of stomach fullness indicated that feeding increased in the final maturity stages. All observations support the hypothesis that energy and nutrients for maturation are supplied mainly by diet rather than by stored resources, but that during maturation there is a shift of emphasis from somatic growth to gonadal development and vitellogenesis. *Sepia pharaonis*, which appears to be an intermittent multiple spawner, does not use protein from muscle tissue for developing and growing its reproduction tissues.

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Cephalopod mollusks have various life history strategies, ranging from typically semelparous (e.g. many coleoids) to iteroparous (e.g. *Nautilus* spp.) (Boyle, 1983, 1987). Different modes of semelparity may occur, and this diversity may be related in part to growth patterns (Mangold et al., 1993). Most cephalopods that have been studied are fast growing, and they generally reproduce once and die (Calow, 1987). However, others have intermittent growth (Boletzky, 1987; Forsythe and Van Heukelem, 1987; Jackson and Choat, 1992) and multiple spawning events (Harman et al., 1989; Lewis and Choat, 1993). We investigated the relation between reproduction and somatic growth in the commercially valuable cuttlefish *Sepia pharaonis* Ehrenberg, 1831.

For many marine invertebrates, reproduction represents an enormous energy investment, and achieving the optimum balance between somatic and reproductive effort is critical to an individual's lifetime fitness (Calow, 1981). The variations in reproductive strategies usually correlate with variations in feeding and growth patterns. Assessing the cost of reproduction is difficult, and although slowing of somatic growth may indicate the allocation of energy to oocyte production, an assessment of somatic tissue may provide a better indicator of the cost of reproduction (Calow, 1983).

For example, in some benthic octopuses, mantle protein is mobilized to provide energy for egg development; the subsequent depletion of protein from body tissues probably contributes to the death of some octopus females (Tait, 1986; Pollero and Iribarne, 1988). This would not seem to be a sensible strategy for a swimming cephalopod, such as cuttlefish, which still requires functional muscle to survive in the water column. *Sepia pharaonis*, which migrates to spawning grounds from its feeding grounds (Gabr et al., 1998), would certainly need to maintain swimming ability.

Elucidation of patterns of energy storage and utilization is important in understanding the interaction between organism and environment (Clarke et al., 1994). Although many studies indicate that oocyte produc-

tion affects the growth and condition of somatic tissue in squid (e.g. Rowe and Mangold-Wirz, 1975; Hatfield et al., 1992), few studies have examined the expenditure of nutrients and energy for the development of reproductive organs in cuttlefish. Boucaud-Camou (1971) found that the digestive gland of *Sepia officinalis* has high concentrations of lipids, suggesting that it acts as a storage organ. Castro et al. (1991) studied changes in the digestive gland of *S. officinalis* and *S. elegans* throughout their life cycles and observed that the digestive gland weight of *S. officinalis* decreased progressively with starvation. However, there is no evidence that the digestive gland provides stored energy for gonad development.

Sepia pharaonis is widely distributed in the Indo-Pacific from the Red Sea to Japan and Australia. Together with *S. dollfusi,* it is the primary fishery in the Suez Canal and the most valuable commercial cephalopod in the northern Indian Ocean (Nesis, 1987). Little is known about the biology of this species (Silas et al., 1985; Aoyama and Nguyen, 1989; Gabr et al., 1998). In this paper, we examine aspects of its life history to determine if a trade-off exists between somatic and reproductive tissues. We measured food intake to determine whether nutritional activity was involved in the development of reproductive organs.

Materials and methods

Samples of *Sepia pharaonis* were collected monthly from Bitter Lake, the main fishing port in the Suez Canal, from September 1994 to April 1996. In total, 1428 females and 1151 males were examined. The dorsal mantle lengths ranged from 10 to 240 mm. Specimens were dissected to determine sex and maturity stage. Four maturity stages for each sex were determined by using a modification of the scale proposed by Mangold-Wirz (1963) and refined in detail for *Sepia pharaonis* by Gabr et al. (1998): for females, I=immature, II=maturing, III=pre-spawning, and IV=spawning; for males, I=immature, II=maturing, III=fully mature, and IV=spawning.

Dorsal mantle length (ML) and nidamental gland length (NGL) of females were measured to the nearest mm. The following measurements of mass were made to two decimal places (in grams): total body mass (BM); total somatic mass (SM); mantle mass (MM); head mass including arms and tentacles (HM); digestive gland mass (DGM); viscera mass (VM) including gills, stomach, caecum, pancreas, ink sac; ovary mass (OM) including oviduct; testis mass (TM); nidamental gland mass (NGM); and spermatophoric complex mass (SCM).

Relative assessment of somatic tissue growth

Two statistical analyses were conducted to determine if somatic tissue declined in relation to size during maturation. All statistical analyses were carried out by using the MINITAB statistical package and all data were $\log_{10}$-transformed.

In the first analysis, a multiple regression was applied to the female data only by using $\log_{10}$ mantle length and $\log_{10}$ nidamental gland length as independent variables. These variables were selected because they correlated with our maturity scale (Gabr et al., 1998). Multiple regression equations were obtained for log-transformed total somatic mass and for masses of mantle, head, digestive gland, viscera, and ovary (including oviduct and oviductal gland, and nidamental gland). This analysis allowed for the use of a continuous variable in the assessment of maturity over the whole size range of the sampled population. This multiple regression analysis was carried out only on females because length was used in the analysis. To carry out a similar exercise with male cuttlefish, the relation of the log-transformed mass of each organ with spermatophoric complex mass (SCM) and body mass would have to be used. These variables would lead to problems in scaling because they would involve autocorrelation, which would distort perceived relationships (LaBarbera, 1989). The ratio of SCM to ML has not been tested before as an objective measure of maturity in male cuttlefish and therefore no analysis was included here.

In the second analysis, a multivariate analysis of covariance (ANCOVA) was applied to the total somatic mass, individual somatic organs, and reproductive organs, whose relationships with the reproductive cycle were considered dependent variables (Garcia-Berthou and Moreno-Amich, 1993). Mantle length was treated as the covariate. A fundamental assumption of standard ANCOVA (McCullagh and Nelder, 1983) is the homogeneity of regression coefficients (slopes) of dependent variable and covariate relationships. This assumption can be tested with a special design of ANCOVA, by analyzing the pooled covariate by factor interaction. If the covariate by factor interaction is significant, standard ANCOVA should not be developed. Otherwise, if the covariant by factor interaction is not significant, the standard ANCOVA design is the preferred method. For the cases with significant effect with factor (maturity stage), the variation can be described by using the predicted means for each cell, adjusted for the effect of the covariate. We set the alpha level for statistical significance at 0.001 to identify the strongest effects of maturity on the dependent variables.

Dry weight analysis

To study the seasonal variation in somatic and reproductive organs, dry weight was used to correct for differences in water content between different organs. The samples for this study were collected from November 1994 to April 1996. From each monthly sample, a subsample of 20 females and 20 males was selected with mantle lengths within a 20-mm size range encompassing the mean size at maturity (the size at which 50% of the individuals were maturing or mature). This size was 122 and 61 mm ML (calculated by using the whole-year sample) for females and males, respectively (Gabr et al., 1998). It is possible to treat specimens from around the mean as "standard" animals (*sensu* Gabbott, 1976) and so compare cuttlefish at different degrees of maturity without having to make statistical corrections for size. There were no cuttlefish of maturity stage I in this subsample; however, stages II to IV were present. The cuttlefish in the subsample were dissected in the same way as those in the sample as a whole. The same measurements of mass to two decimal places (in grams) were taken, but dry rather than wet weight was used. Tissues were dried to constant weight (for 48 h) at 80°C and then cooled in a desiccator.

The following indices were calculated for dry weight tissues: gonadosomatic index for females (GSI) = 100 OM/BM; gonadosomatic index for males (GSI) = 100 TM/BM; nidamental gland index (NGI) = 100 NGM/BM; spermatophoric complex index (SCI) = 100 SCM/BM; mantle index (MI) = 100 MM/BM; head index (HI) = 100 HM/BM; digestive gland index (DGI) = 100 DGM / BM, and viscera index (VI) = 100 VM/BM.

Analysis of protein

The dry tissue of mantle and whole head for 7 to 9 females of maturity stages II–IV was ground to a fine powder with a mortar and pestle. The powdered samples were placed in sealed plastic vials and stored for further analysis. The Kjeldahl method for determination of nitrogen was used (see Giese, 1967). % Protein = % nitrogen × 6.25 (Giese, 1967; Rigby, 1990; Dickey-Collas, 1991). Kruskal-Wallis ANOVA was used to examine the significant variation in percentage of protein between maturity stages.

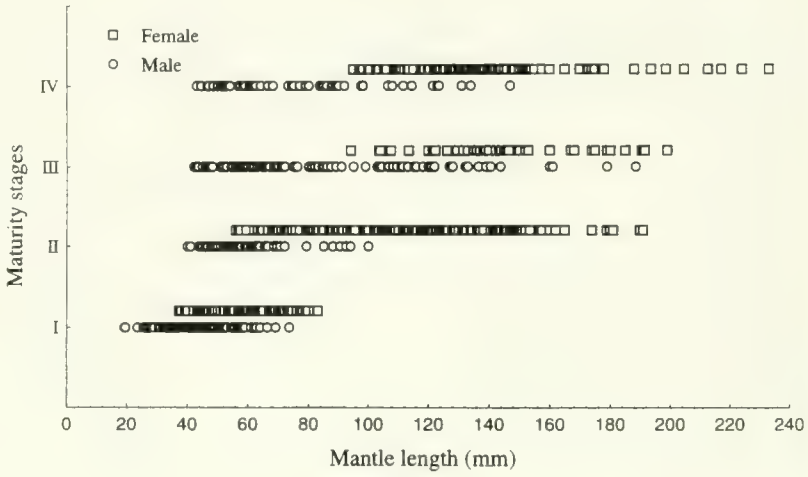

Figure 1

Relation between mantle length and maturity stages in female and male *Sepia pharaonis*.

Stomach content analysis

Each specimen's stomach fullness was estimated according to a 5-level subjective scale: 0=empty; 1=one-quarter full; 2=half full; 3=three-quarters full; 4=full or distended.

Length-weight relationship

Equations of the form $BW = aML^b$, where a and b are constants of the regression, were fitted by transforming the data into $\log_{10}$ and deriving the regression line by the least squares method. Correlation was expressed by the coefficient r^2, and comparisons between males and females were made by ANCOVA.

Results

Growth and maturity

Maturity generally increased with mantle length, but each stage was represented by a very wide range of mantle lengths with considerable overlap between stages (Fig. 1). This finding suggests that there is no strong relation between growth and maturation rate. Males attained full maturity (stage III) at a smaller size than females (stages III and IV).

Maturity stages versus soma production and gonad production

In females (Table 1), there was a significant increase in total somatic mass and mass of somatic organs

Table 1

Intercepts (a) and slopes (b_1 and b_2) ± SD for multiple regression equations relating mantle length (b_1) and nidamental gland length (b_2) to tissue masses for female *Sepia pharaonis*. The equation is log tissue mass = $a + b$, log $ML + b_2$ log NGL. P is level of significance (* indicates significant relationships i.e. $P<0.05$); s is residual standard deviation about the regression lines; r^2 is adjusted proportion of variation accounted by the variance model; and n is number of specimens.

	a	b_1	P	b_2	P	s	r^2	n
Independent variables:	mantle length; nidamental gland length							
Dependent variables:	0.0001*							
Total somatic mass	−0.87 ±0.05	2.92 ±0.04	0.0001*	−0.09 ±0.02	0.0001*	0.24	0.99	191
Mantle mass	−1.22 ±0.05	2.98 ±0.05	0.0001*	−0.14 ±0.02	0.0001*	0.59	0.98	226
Head mass	−1.21 ±0.04	2.84 ±0.04	0.0001*	−0.08 ±0.02	0.005*	0.25	0.99	191
Digestive gland mass	−2.20 ±0.10	2.98 ±0.11	0.0001*	−0.02 ±0.05	0.690	1.78	0.93	192
Viscera mass	−1.71 ±0.03	2.58 ±0.13	0.0001*	0.03 ±0.06	0.580	2.4	0.89	192
Ovary mass	0.49 ±0.36	−1.66 ±0.41	0.001*	3.50 ±0.16	0.0001*	17.33	0.93	176
Nidamental gland mass	−0.17 ±0.26	−0.65 ±0.29	0.030	2.92 ±0.11	0.0001*	9	0.96	176

(i.e. mantle, head digestive gland and viscera masses) with mantle length ($P<0.05$). The effect of ML on reproductive organ mass (i.e. ovary, nidamental gland masses) also was significant ($P<0.05$). In relation to nidamental gland length, there was a small but significant decrease ($P<0.05$) in total somatic mass, mantle mass, and head mass, whereas the relative decrease in digestive gland mass and viscera mass was not significant ($P>0.05$). As expected, there was also a highly significant increase ($P<0.05$) in reproductive organ mass with maturity (NGL).

The second analysis was an analysis of multivariate covariance (ANCOVA). In an animal that matures at a wide range of body sizes, it is difficult to quantify the pattern of maturation because comparisons of individuals of different sizes cannot be thought of as indicating the pattern of growth and maturation of any one animal. Thus, although some animals matured at 60 mm ML, others remained immature at larger sizes (Fig.1). ANCOVA corrects for the variation in size (ML) of animals within maturity stages.

Table 2 shows the initial standard ANCOVA design to test for homogeneity of slopes. In females, there was significant effect of an interaction between the factors (maturity stage) and covariate (mantle length) for OM and NGM. The effect of interaction of mantle length and maturity stages on TSM, MM, HM, DGM, and VM was not significant ($P>0.001$). Thus in these cases the hypothesis of homogeneity of slopes was accepted; therefore further analyses were required to test the effect of maturity stages for these variables. In males, there was a highly significant effect ($P<0.001$) between mantle length and maturity stage for all log-transformed dependent variables except spermatophoric complex mass. Thus for these variables the hypothesis of homogeneity of slopes was rejected and further analysis was not possible (i.e. the standard ANCOVA design should not be developed for these cases).

The results of the final ANCOVA design (in the cases where the effect of mantle length and maturity stage interactions were not significant) are indicated in Table 3. In female *Sepia pharaonis*, maturity significantly affected TSM, MM, HM, and VM ($P<0.001$) but did not significantly affect DGM ($P>0.001$). In males, maturity significantly influenced spermatophoric complex mass ($P<0.001$).

Figure 2 shows the adjusted means for each dependent variable for each maturity stage after the removal of the mantle length (covariate) effect when the effects of maturity stages were found to be significant. For females, there was a decrease in total somatic mass, mantle mass, and head mass with increasing maturity stage. There was a decrease in viscera mass from stage I to stage III followed by an increase at stage IV (Fig. 2A). For males, there was an increase in relative mass of spermatophoric complex mass with increasing maturity stage (Fig. 2B).

Monthly variation in soma versus gonad production

Monthly fluctuations in mean dry weight indices for individual organs of somatic tissue (mantle index, MI; head index, HI; digestive index, DGI; and viscera index,VI) and reproductive tissue (gonadosomatic index, GSI; nidamental gland index, NGI; and spermatophoric complex index, SCI) for females and males are illustrated in Figures 3 and 4, respectively. These indices displayed monthly fluctuations and indicated the relative proportion that each body component contributed to the weight of the entire body. The mantle mass was always the largest component

Table 2

Preliminary design of ANCOVA for *Sepia pharaonis*. In each case, mantle length is the covariate, maturity stage (I–IV) is the factor, and the dependent variables are total somatic mass (TSM), mantle mass (MM), head mass (HM), digestive gland mass (DGM), viscera mass (VM), ovary mass (OM), nidamental gland mass (NGM), testis mass (TM), and spermatophoric complex mass (SCM). The homogeneity of slopes was tested with a pooled covariate by factor interaction: *F*-statistic. Significance levels ($P<0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)		ML × MSt	
	F	*P*	*F*	*P*	*F*	*P*
Female						
TSM	11000.00	<0.001*	2.80	0.039	1.87	0.130
MM	11000.00	<0.001*	4.74	0.003	2.81	0.030
HM	10000.00	<0.001*	5.29	0.001	3.93	0.009
DGM	3440.00	<0.001*	2.18	0.089	2.16	0.092
VM	2926.30	<0.001*	0.40	0.754	0.98	0.400
OM	271.07	<0.001*	25.15	<0.001*	29.87	<0.001*
NGM	513.73	<0.001*	166.10	<0.001*	317.58	<0.001*
Male						
TSM	918.60	<0.001*	22.00	<0.001*	23.00	<0.001*
MM	1745.94	<0.001*	14.32	<0.001*	13.66	<0.001*
HM	1295.97	<0.001*	12.50	<0.001*	11.02	<0.001*
DGM	849.18	<0.001*	11.15	<0.001*	9.55	<0.001*
VM	853.13	<0.001*	5.96	<0.001*	5.28	<0.001*
TM	612.65	<0.001*	294.18	<0.001*	15.52	<0.001*
SCM	749.19	<0.001*	6.01	<0.001*	0.88	0.450

proportionally, followed by the head mass. Thus, *S. pharaonis* weight gain and loss were accounted for mainly by the mantle and head mass that underwent fluctuation in mean dry weight index during the study.

The MI and HI diminished considerably as gonad development proceeded. The largest decrease in MI and HI of females occurred in spring and summer (from March to September), as shown in Figure 3. These indices decreased from 52% to 41% and from 34% to 28%, respectively. In contrast, during the same period the gonads (GSI, NGI) exhibited development; GSI increased from 1% to 9% and NGI increased from 2% to 7%. VI increased rapidly from May to November, from 5% to 10%. DGI showed little change over the whole sampling period (ranging between 7% and 10%).

By contrast, in male *Sepia pharaonis*, the MI, HI, and DGI remained relatively constant throughout the entire sampling period (Fig. 4). The pattern of VI was consistent with the situation in female, increasing from 5% to 8% during the period from May to October. There was a gradual increase in GSI and SCI from November, reaching the highest value in May (≈1.3%), and spawning after June was indicated by a decline in GSI and SCI.

Table 3

Final design of ANCOVA for *Sepia pharaonis* data for which the homogeneity hypothesis was accepted, *F*-statistics, and *P*-values. See Table 2 for definitions of abbreviations. Significance levels ($P<0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)	
	F	*P*	*F*	*P*
Female				
TSM	15000.00	<0.001*	25.130	<0.001*
MM	16000.00	<0.001*	40.570	<0.001*
HM	14000.00	<0.001*	10.470	<0.001*
DGM	4770.00	<0.001*	0.680	0.560
VM	4031.89	<0.001*	11.270	<0.001*
Male				
SCM	901.800	<0.001*	133.890	<0.001*

Percentage of protein, water content, and maturity stage

The mean percentage composition of protein and mean percentage of water content in the mantle and head of females for maturity stages II–IV is shown

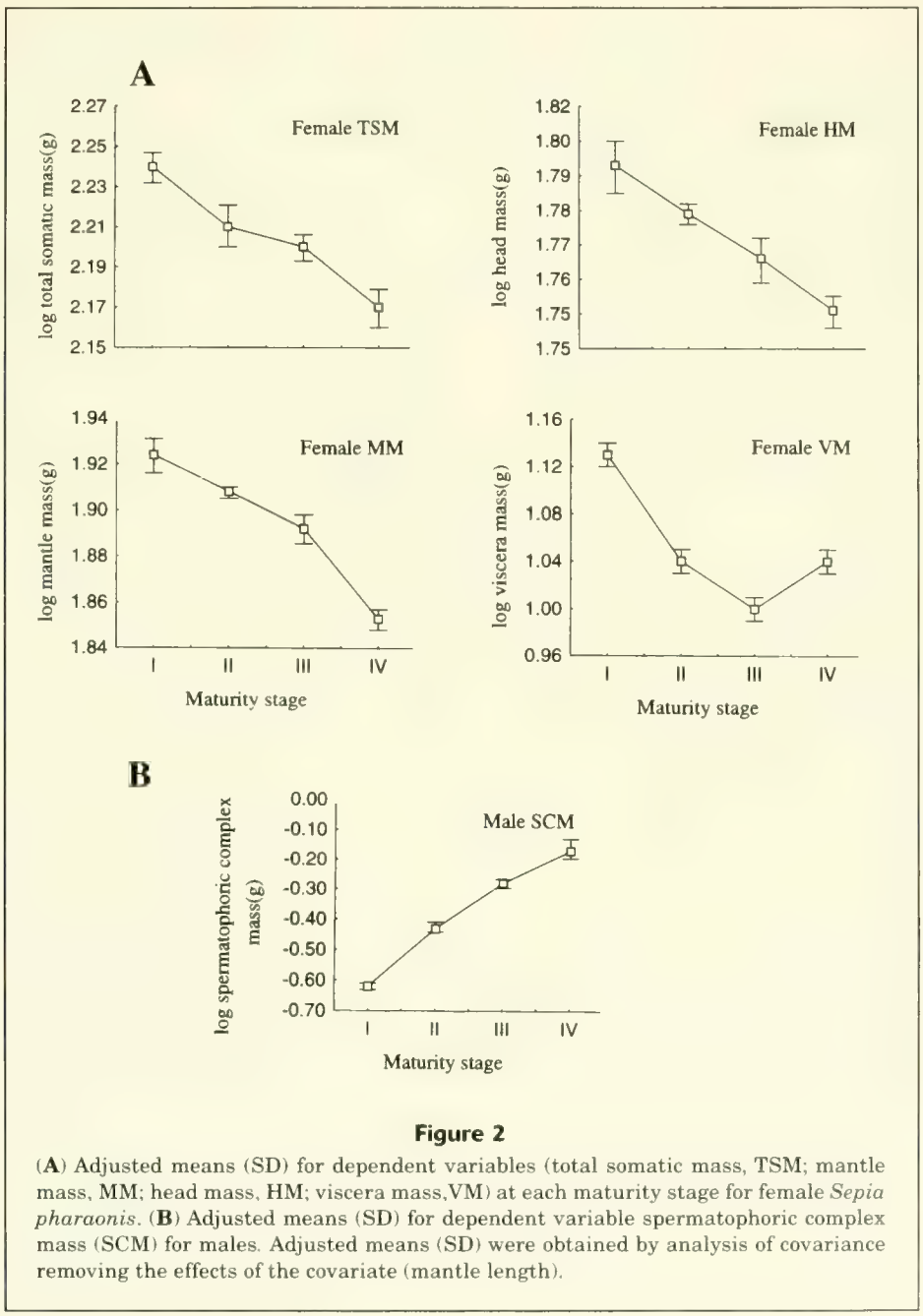

Figure 2

(**A**) Adjusted means (SD) for dependent variables (total somatic mass, TSM; mantle mass, MM; head mass, HM; viscera mass,VM) at each maturity stage for female *Sepia pharaonis*. (**B**) Adjusted means (SD) for dependent variable spermatophoric complex mass (SCM) for males. Adjusted means (SD) were obtained by analysis of covariance removing the effects of the covariate (mantle length).

in Table 4. In neither mantle nor head was there significant variation ($P>0.05$) in percentage of protein or water content with maturity stage.

Stomach fullness in relation to maturity stages

The stomach fullness for each maturity stage for each sex is illustrated in Figure 5. The degree of stomach fullness remained relatively constant through the maturity stages, indicating that *Sepia pharaonis* continued to feed when mature.

Length-weight relationship

The length-weight relationship for *Sepia pharaonis* is described by the equation: $Wt = 0.27L^{2.65}$, $r^2 = 0.99$, $n = 966$ for females, and $Wt = 0.28L^{2.60}$, $r^2 = 0.99$, $n = 723$ for males. The elevation and slopes from the regression equations for females and males did not differ significantly, thus indicating that females have approximately the same weight as males at the same mantle length, and that both sexes increase similarly in weight per unit gain in mantle length.

Discussion

This study describes the pattern of allocation of resources to the growth of somatic and reproductive tissues in *Sepia pharaonis*, one of the two most commercially important cephalopods in the Suez Canal and northern Indian Ocean. This study indicates that gametogenesis is fueled by energy and nutrients derived from the diet rather than from reallocation of somatic reserves. Two complementary methods (analysis of covariance and multivariate regression on the entire data set) and the monthly changes in dry weight of somatic indices of a restricted size range showed essentially similar patterns of maturation.

Sexual maturation in *Sepia pharaonis* affected males and females differently. Forsythe and Van Heukelem (1987) suggested that male maturity in cephalopods was achieved at little cost to somatic growth and that, in most cases, males continue to grow after reaching maturity. Changes in male somatic mass do not appear to be related to maturity. At full maturity in males, dry weight of reproductive and accessory reproductive tissues accounted for only 2.6% of the total somatic dry weight. However, these tissues accounted for approximately 16% in females. For both sexes, somatic growth was completed by late October as the average mantle mass and head mass components reached maximum weights.

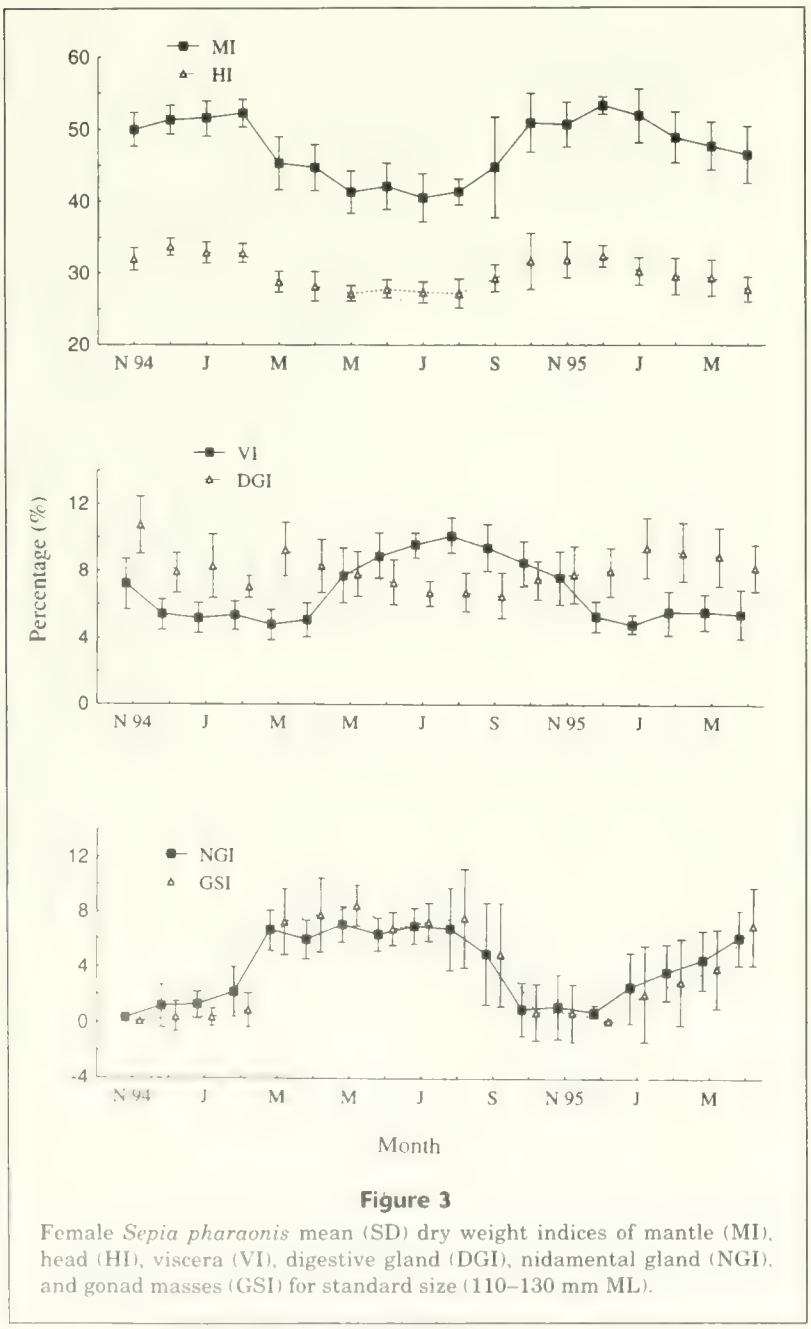

Figure 3

Female *Sepia pharaonis* mean (SD) dry weight indices of mantle (MI), head (HI), viscera (VI), digestive gland (DGI), nidamental gland (NGI), and gonad masses (GSI) for standard size (110–130 mm ML).

In females, spawning occurred from spring throughout the summer, and the end of spawning activity was reflected by a sharp drop in the average gonad weight index in October (Fig. 3) . Thus spawning occurred at the time of increasing temperature and food availability (Gabr, unpubl. data). There was no evidence of decline in feeding rate with maturation. This finding suggests that gonadal growth may be supported directly by the assimilated food ration, although some diversion of resources into reproduction at the expense of somatic growth also occurred. This diversion of resources was indicated by a small but significant decrease in mantle and head mass with maturation (Fig. 2), and the inverse relationship of mantle and head mass with gonadal indices (Fig. 3).

There is some evidence to support the idea that female *Sepia pharaonis* may feed, grow, and mature simultaneously in the field. For example, no spent females were caught at any time of the year. This may be because it is difficult to differentiate spent females from mature ones if spent females remain in good condition (because they continue to feed when mature). Because females need a greater energetic reserve for reproduction, they grow faster than males and reach a maximum size of 240 mm ML, whereas the maximum size for males was 170 mm ML. *Sepia pharaonis* spawns in shallow water and migrates

offshore after spawning either to die or to return to spawn again; such a migration is unlikely to be preceded by any degradation of mantle muscle, which is the major organ for locomotion in cuttlefish. In neither mantle nor head was there a significant variation in percentage of protein or water content with maturity stage. These data indicate that female *S. pharaonis* possibly do not use mantle or head tissue to fuel gonadal development, at least during the beginning of the spawning season.

In sharp contrast, studies of another cuttlefish, *Sepia dollfusi* (Gabr et al., in press), have demonstrated that this species seems to use mantle muscle as an energy source during gonadal development. There thus appears to be a continuum in cuttlefish reproductive strategy. At one end, spawning is associated with gonad maturation at the expense of somatic tissue. At the other end, growth of reproductive organs takes place through the use of energy and nutrients derived from the diet, not through mobilization of nutrients and energy from somatic tissue.

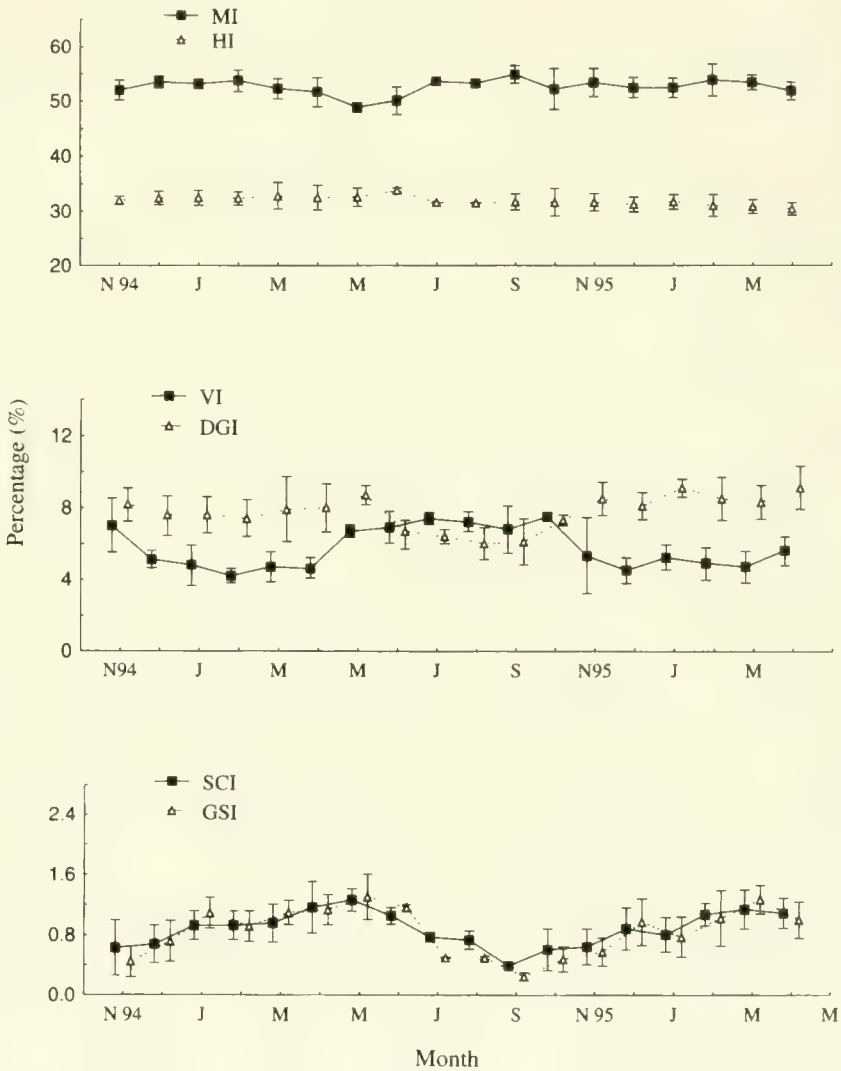

Figure 4

Male *Sepia pharaonis* mean (SD) dry weight indices of mantle (MI), head (HI), viscera (VI), digestive gland (DGI), spermatophoric complex (SCI) and gonad masses (GSI) for standard size (50–70 mm ML).

The results of this paper agree with some studies on the squid *Illex argentinus* (Hatfield et al., 1992; Rodhouse and Hatfield, 1992; Clarke et al., 1994). Although mantle mass of female *Illex argentinus* decreases in relation to ML with maturity, this is not associated with degradation or changes in the biochemical composition of mantle muscle. Studies on *Loligo forbesi* (Collins et al., 1995), *L. gahi* (Guerra and Castro, 1994) and *Photololigo* sp. (Moltschaniwskyj, 1995) have also demonstrated that maturation and growth occur simultaneously during most of the life cycle and that the condition of the squid remains high at maturation.

The digestive gland showed no loss of mass during maturation. Boucaud-Camou (1971) indicated that the digestive gland of *Sepia officinalis* could act as a lipid storage organ, and Blanchier and Boucaud-Camou (1984) found that the variation in lipid levels of the digestive gland seemed more related to diet than to sex or maturity state of the gonads. There was no significant variation in the digestive gland weight with maturity state and season. Thus, the digestive gland mass cannot be used as an indicator of feeding activity in *S. pharaonis* as it can in some squid (Abolmasova et al., 1990) because no increase in DGI was found in the season of high feeding activity. This agrees with Castro et al. (1991), who found no significant variation in the digestive gland weight with season in *S. officinalis* and *S. elegans*.

In conclusion, this study shows that the pattern of intermittent spawning suggested by our previous

Table 4

Summary of mean ± SD values of percentage of protein and water content in mantle and head dry tissue with maturity stages for female *Sepia pharaonis*.

		% Protein			% Water content	
Maturity stage	Number	Mantle	Head	Number	Mantle	Head
II	9	78.33 ±0.68	76.21 ±0.32	66	75.83 ±1.4	79.38 ±1.4
III	8	79.78 ±0.41	76.23 ±0.39	20	76.18 ±1.3	79.64 ±1.06
IV	7	78.19 ±0.39	75.82 ±0.53	79	75.48 ±1.8	78.91 ±1.5
Kruskal-Wallis ANOVA:	*H*	2.08	0.24		1.32	3.37
	P	0.35	0.88		0.51	0.18

study of this species (Gabr, et al., 1998) is quite likely, partly because the spawning season is greatly protracted (Fig. 3). Indeed, it appears that this species is capable of meeting the demands of oocyte production without metabolizing reserves of other tissues. Both males and females continue to feed as maturity is reached, thus energy for gonad production is diverted primarily from the food supply, although some diversion from somatic tissue may also occur. In the context of this paper and results from *S. dollfusi* (Gabr et al., in press), variation in reproductive strategies correlates with variations in feeding and growth patterns as suggested previously for other coleoids (Mangold et al., 1993).

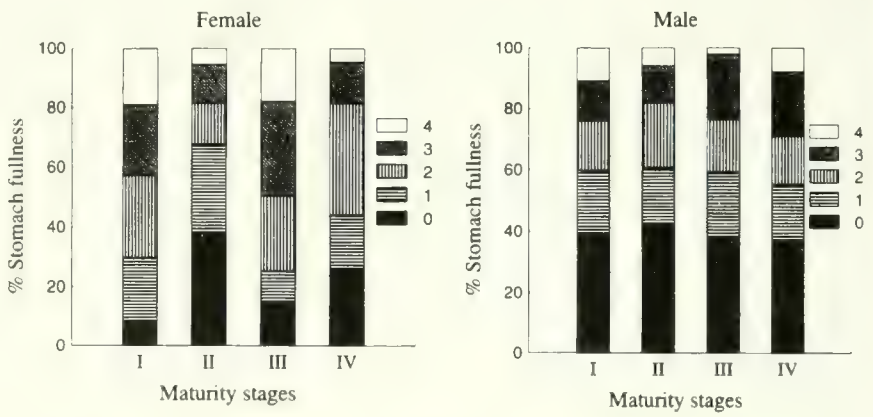

Figure 5

Stomach fullness for each maturity stage of both sexes of *Sepia pharaonis*. 0 = empty; 1 = one-quarter full; 2 = half full; 3 = three-quarters full; 4 = full or distended).

Acknowledgments

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Aging methods for yellowtail kingfish, *Seriola lalandi*, and results from age- and size-based growth models

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Abstract.—Dorsal spines, otoliths, scales, and vertebrae collected from yellowtail kingfish (*Seriola lalandi*) in NSW, Australia, were assessed for usefulness in estimating age. Legibility of growth zones, the time scale at which zones form, and precision of age estimates were evaluated for fish sizes from 323 to 1090 mm FL. All calcified structures contained growth zones, but dorsal spines were unsuitable for age determination because it was likely that early growth zones were lost. From marginal increment analysis, it appeared that one zone was laid down per year for otoliths and possibly scales, but a clear pattern was not found for vertebrae. Although exact agreement between repeated age readings was relatively low (50–66%), agreement within one zone was higher (92–96%) and scales provided the most precise readings. Precision decreased with increasing age of fish. Growth curves derived from otoliths and scales were similar for all ages except fish from the first age class; those derived from otoliths and vertebrae were similar for all fish with less than eight growth zones. Although statistical differences were found between the growth curves of scales and vertebrae for some age classes, with the exception of the first age class these differences were not biologically important. Growth rates estimated from length-frequency (age-based) and mark-recapture (length-based) data compared favorably with those estimated from calcified aging structures. Otoliths, scales, and vertebrae all showed promise as structures for aging kingfish, but further work is needed to determine the position of the first zone and to validate estimates for all age classes. Until such work is completed, we recommend that scales and either otoliths or vertebrae be used for aging kingfish.

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Yellowtail kingfish, *Seriola lalandi*, is a popular recreational species and supports significant commercial fisheries throughout temperate regions of the world. In Australia, the major commercial fishery for yellowtail kingfish is in New South Wales where 400–600 tonnes are caught per year. Despite the existence of a commercial fishery and persistent controversy about exploitation of the species, very little is known about its biology. For future management of the fishery and for stock assessment purposes, information on age and growth is needed.

Estimates of age of *Seriola* spp. have been derived from a variety of methods and structures, reflecting the difficulty of aging *Seriola* and other pelagic species. The Japanese species (*Seriola quinqueradiata*) is the most studied species in the genus because of its importance in aquaculture. Studies in the 1950s used scales, vertebrae, and opercular bones for aging (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959). More recent studies have focused on the use of vertebrae (e.g. Munekiyo et al., 1982; Murayama, 1992). Scales have also been used to age *S. lalandi* (formerly *S. dorsalis*, Baxter, 1960), as have otoliths (Penney[1]). Recently, sectioned otoliths were used to determine ages of *Seriola dumerili*, although it was acknowledged that age and growth determinations were difficult (Manooch and Potts, 1997). Despite the use of a variety of structures for aging *Seriola* spp., there has been no comparative analysis to determine which structure provides the most reliable estimates. In addition, most studies have assumed that growth zones are annual and there have been few validations of age estimates (but see Mitani and Sato, 1959; Baxter, 1960).

The specific objectives of this study were 1) to assess the usefulness of several structures (scales, otoliths, dorsal spines, and vertebrae) for determining the age of kingfish, 2) to compare multiple age estimates for different structures in order to determine the most precise method for determining age and growth parameters, 3) to provide information on size-at-age and 4) to compare growth rates obtained

[1] Penney, A. J. 1992. Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa. Personal commun.

from age-length data (from counts of zones in calcified structures) to those obtained from length-frequency and mark-recapture (tagging) data. We acknowledge that the data from these three approaches for estimating growth are not directly comparable (Francis, 1988a), but follow the recommendations of Francis (1995) in interpreting differences.

Materials and methods

Fish collection and treatment

Yellowtail kingfish, *Seriola lalandi*, specimens were collected from New South Wales, Australia, between August 1995 and July 1996 by commercial or recreational fishermen. Fish caught by commercial fishermen were obtained after being processed by filleting. Fish were measured (total length, fork length) and sagittal otoliths, dorsal spines, scales, and vertebrae removed. Dorsal spines were examined but considered unsuitable for aging because the center (core) region was either occupied by vascular bony tissue or was hollow. The hollow core in large fish was found to have a larger diameter than the whole spine of small fish. For this reason, it was likely that early growth zones were lost in older fish and therefore spines were considered unsuitable for aging.

Sagittae

Whole sagittae were burned for 7 min at 500°C. They were viewed under a low-power dissecting microscope (6× magnification) with reflected light against a black background. Assignments of age were based on counts of opaque (light) zones or ridges (or both) that were usually most visible at the base of the rostrum on the ventral surface (Fig. 1A). Sagittae were also embedded in clear resin, sectioned in a transverse plane with a low speed saw, the sections (≈350 mm thickness) mounted on glass slides, and viewed under a compound microscope (40× magnification) with reflected light against a black background.

Scales

Scales were removed from a position anterior and ventral to the pectoral fin. It was necessary to remove scales from such a position because most fish had been processed prior to the removal of scales. Scales from each fish were soaked in a solution of sodium hydroxide for 3 h, then rinsed and soaked in water for a further 3–12 h. Clean, nonreplacement (i.e. original scales showing typical ctenoid shape) scales were dry-mounted between two glass microscope slides. Scales were read under a compound microscope (20× magnification) with reflected light against a black background. Presumed annuli were identified by cutting over (*sensu* Bagenal and Tesch, 1978) in the lateral fields or by clear zones, where circuli were more widely spaced, in the anterior field.

Vertebrae

The second vertebra of 24 vertebrae present in kingfish was chosen because it was most easily obtained from processed fish. Vertebrae were either stored frozen with flesh intact, or the flesh was removed, and the vertebrae were separated from each other and stored dry. The spines were removed and each vertebra cut in half along the longitudinal–horizontal plane and stained in a solution of alizarin red S (following Berry et al., 1977) for 8 h, rinsed in tap water for at least 1 min, and dried at room temperature. Vertebrae were read under a dissecting microscope (6–12× magnification) with reflected light from a blue-filtered, high-intensity bulb against a black background. Age was estimated from counts of ridges on the inner surface of the vertebra from the core to the outer edge of the centrum (Fig. 1C).

Assessment of aging techniques

To determine whether the zones would be reliably interpreted, two replicate counts of zones were made for each structure by the same person. Counts were usually separated by one month. All readings were done in a random order, with no knowledge of date of collection, size of fish, or knowledge of previous counts. Preliminary investigations of transverse sections of otoliths from 50 fish (ranging from 323 to 1090 mm FL) found that growth zones were not interpretable for any fish (Fig. 2).

Multiple counts of zones (two counts for each aging structure) were used to estimate the probability of assigning an age a to a fish with estimated "true" age b following maximum-likelihood estimation procedures outlined in Richards et al. (1992). This procedure requires the estimation of a classification matrix where there are columns for each "true" age and rows for each assigned age, and the entries refer to probabilities of assigning age a to a fish, given its true age b. "True" age is best described as the most probable age, and it does not refer to the accuracy of the age estimate nor does it substitute for age validation procedures. It is assumed that fish will be assigned to the true (or most probable) age class with the highest probability (Richards et al., 1992).

The classification matrix is defined by up to four parameters, where the first two parameters, σ_1 and

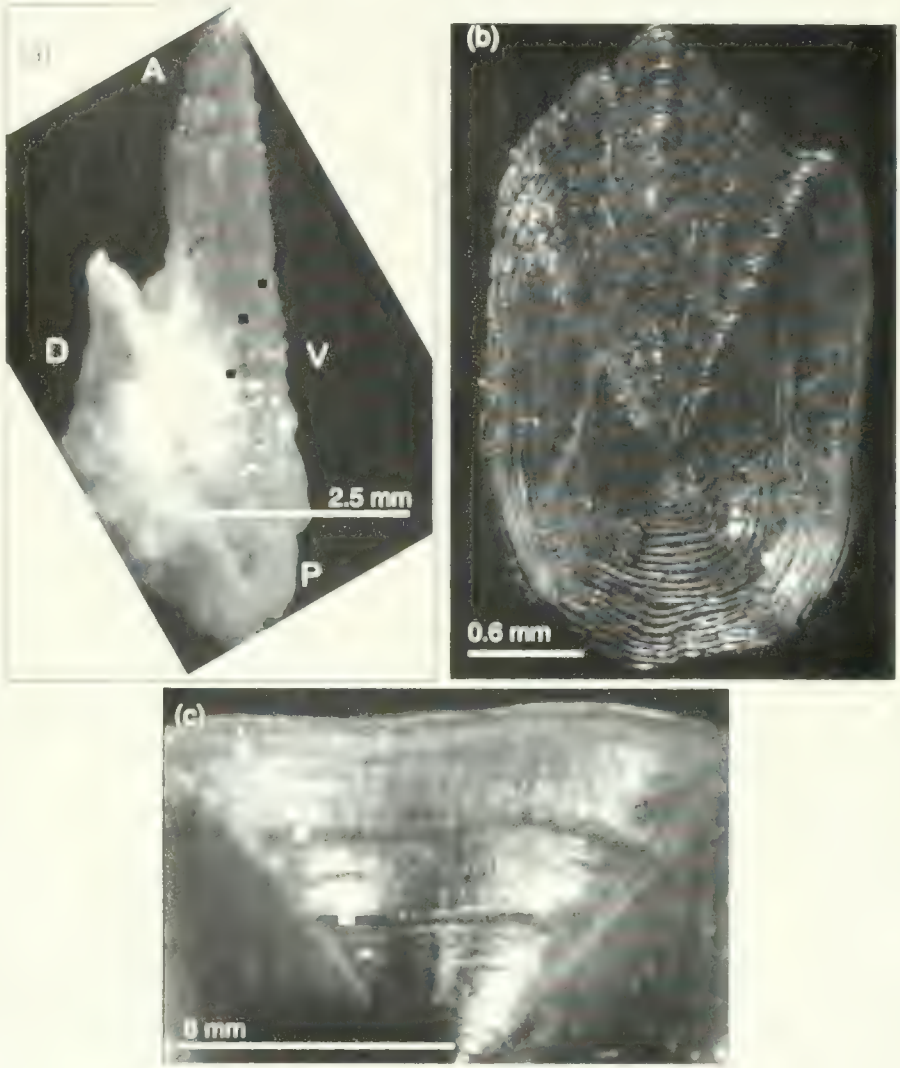

Figure 1

Structures used to estimate the age of kingfish from New South Wales: (**A**) otolith (860 mm FL, age 3); (**B**) scale (618 mm FL, age 3); and (**C**) vertebra (720 mm FL, age 3). All structures viewed with reflected light against a black background. Size of scale bars are indicated on each figure. Growth zones are indicated by squares; abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral.

σ_A, are estimates of the standard deviation for the observation a at age 1 and A respectively. The third parameter, α, determines nonlinearity of $\sigma(b)$, the standard deviation of the observation a. The fourth parameter, β, controls the extent that the classification matrix may be dominated by its diagonal entries (Richards et al., 1992). Two possible representations of the classification matrix were used, namely a normal and an exponential representation (*sensu* Richards et al., 1992, p. 1803) and the α parameter was constrained to 0 during one fit of each of the normal and exponential representations, allowing four different cases of the model to be fitted for each aging structure. The appropriate model structure, or best fit model, for the classification matrix was then selected by using the Akaike information criterion (AIC) where a model with a low AIC value in relation to other models was considered to provide a good fit (Richards et al., 1992).

Initially, data from each aging structure (otoliths, scales, and vertebrae) were analyzed separately and an age assigned to each fish from each structure. The

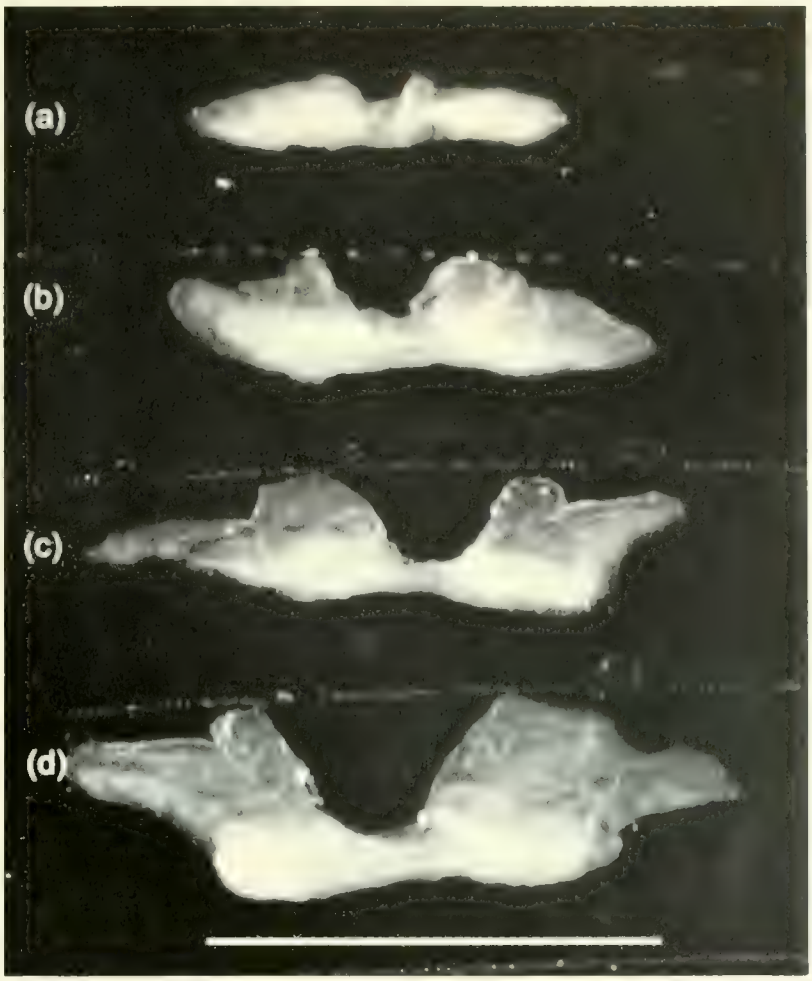

Figure 2

Transverse sections of sagittal otoliths of kingfish over a range of sizes viewed with reflected light against a black background: (**A**) 337 mm FL; (**B**) 638 mm FL; (**C**) 850 mm FL; and (**D**) 1002 mm FL fish. Scale bar is 1.5 mm.

classification matrix for the best model (see above) was used to estimate the most probable age of each fish by determining the probability that a fish would be from each true age class given its two assigned ages. Each fish was assigned to the age class with the highest probability (Richards et al., 1992). This estimate of age was used for growth models. Only the first five age classes (0–4) were used in the classification matrix because, although older fish occurred, sample sizes were small and some extrapolation for missing age classes would be necessary. Because data from older fish are important in estimating growth models, fish not used in the classification matrix were assigned an age by randomly selecting one of their two age readings.

The data matrix comprising the two age readings for each of the three aging structures was then examined to determine possible effects of the different aging structures and to determine a final age for each fish. Classification matrices for each aging structure were determined following a modification of the methods of Richards et al. (1992; outlined above). Results from running the models for each structure separately showed that the model of best fit was obtained by using a normal model with $\alpha = 0$; therefore, in its simplest form, the model contained the parameters σ_1, σ_A, and terms for the relative bias of each method (r_1 and r_2; $r_3 = 0 - r_1 - r_2$). Parameters determining the change in bias with age (γ) and nonlinearity of bias with age (η) were also added alone and indexed by aging structure. Different combinations of the model parameters were therefore tested to determine which model provided the best fit to the data and to determine relative biases by method.

Table 1

Summary of the different cases of Schnute's (1981) size-at-age growth model that was fitted to age estimates from different calcified structures and Francis's (1995) mark-recapture analogue of Schnute's growth model that was fitted to the tagging data.

	Schnute's (1981) size at age model	Francis's (1995) mark-recapture analogue of Schnute's (1981) growth model
Case 1: a≠0, b≠0	$Y(t)=\left[y_1^b+(y_2^b-y_1^b)\frac{1-e^{a(t-\tau_1)}}{1-e^{a(\tau_2-\tau_1)}}\right]^{\frac{1}{b}}$	$\Delta Y=-Y_t+\left[Y_t^b e^{-a\Delta t}+c(1-e^{-a\Delta t})\right]^{\frac{1}{b}}$
Case 2: a≠0, b≠0	$Y(t)=y_1\exp\left[\log(y_2/y_1)\frac{1-e^{a(t-\tau_1)}}{1-e^{a(\tau_2-\tau_1)}}\right]$	$\Delta Y=-Y_t+Y_t^{\exp(-a\Delta t)}\exp\left[c(1-e^{-a\Delta t})\right]$
Case 3: a≠0, b≠0	$Y(t)=\left[y_1^b+(y_2^b-y_1^b)\frac{t-\tau_1}{\tau_2-\tau_1}\right]^{\frac{1}{b}}$	$\Delta Y=-Y_t+\left[Y_t^b+(\lambda_1^b-y_1^b)\Delta t\right]^{\frac{1}{b}}$
Case 4: a≠0, b≠0	$Y(t)=y_1\exp\left[\log(y_2/y_1)\frac{t-\tau_1}{\tau_2-\tau_1}\right]$	$\Delta Y=-Y_t+Y_t(\lambda_1/y_1)^{\Delta t}$

Meaning of terms

$Y(t)$ = fish size (FL) at age t, τ_1 and τ_2 = lower and upper ages of fish respectively where $\tau_2 > \tau_1$, y_1 and y_2 = mean sizes at ages τ_1 and τ_2, respectively. a and b describe the shape of the curve.

ΔY = mean growth

Y_t = size at marking

y_1 and y_2 = lower and upper sizes of fish, respectively, where $y_1 < y_2$

g_1 and g_2 = mean annual growth for fishes of sizes y_1 and y_2 respectively,

b = describes curvature in model,

$\lambda_1 = y_1 + g_1$ and $\lambda_2 = y_2 + g_2$,

$$a=\ln\left[\frac{y_2^b-y_1^b}{\lambda_2^b-\lambda_1^b}\right] \text{ if } b\neq 0 \text{ or}$$

$$a=\ln\left[\frac{\ln(y_2/y_1)}{\ln(\lambda_2/\lambda_1)}\right] \text{ if } b=0,$$

$$c=\frac{y_2^b\lambda_1^b-y_1^b\lambda_2^b}{\lambda_1^b-y_1^b+y_2^b-\lambda_2^b} \text{ if } b\neq 0 \text{ or}$$

$$c=\frac{\ln(y_2)\ln(\lambda_1)-\ln(y_1)\ln(\lambda_2)}{\ln(\lambda_1/y_2)-\ln(\lambda_2/y_1)} \text{ if } b=0, \Delta t=1$$

To determine the timing of zone formation, the edges of the various structures were examined. The growth of the structure, subsequent to the most recent zone, was estimated as a percentage (20, 40, 60, and 80%) of the previously completed zone. It was also noted whether the zone was considered to be on the edge of the structure. Only fish with 2–4 growth zones were used. Fish were examined individually by structure in a random order with no knowledge of date of collection.

Estimation of growth models from calcified structures

Growth models using age estimates from different calcified structures were derived by using procedures outlined in Schnute (1981). Schnute's model relates size (FL) to age by several parameters, including two that describe the shape of the curve (a and b; Table 1). These latter parameters combine to describe a range of common growth curves, including the von Bertalanffy ($a>0$, $b=1$), Richards ($a>0$, $b<0$), logistic ($a>0$, $b=-1$) and Gompertz ($a>0$, $b=0$) (Table 1; Schnute, 1981). The other parameters in Schnute's growth model were y_1 and y_2, the mean sizes at ages τ_1 and τ_2 respectively, where the value of τ_1 and τ_2 are specified, but usually chosen to be near the lower and upper ends of the range of ages in the data. In this study, τ_1 and τ_2 were set at 1 and 5 respectively. All growth models were calculated by minimizing sums of squares and using additive errors because variation in size-at-age was similar for all ages of fish (see "Results" section).

Initially, a two-parameter model (y_1 and y_2) was fitted to the data (case 4 in Table 1). Two types of a three-parameter model [parameters were a, y_1, and y_2 (case 2), and b, y_1, and y_2 (case 3)] and a four-

parameter model (a, b, y_1, and y_2, case 1) were then fitted to the data (Table 1). To determine whether the addition of extra parameters resulted in a significantly better fit, significance tests based on the F-distribution were used (Schnute, 1981). Where the same number of parameters were present in the models (e.g. comparison of the two models with three parameters), the model with the lowest residual sums of squares was selected as the best fit.

Estimation of rates of growth from tagging data

Seriola lalandi tagged as part of the NSW Fisheries Gamefish Tagging program (Pepperell, 1985, 1990) were used to estimate growth. A major limitation of these data were that measurement methods were not standard and some measurements appeared spurious. Although most anglers measured total length, some measured fork length only. Where this occurred (17% of fish), fork length (mm) was converted to total length with the equation TL (mm)=1.122 × FL + 9. This equation was calculated from fish obtained for aging in which both fork and total lengths were measured (n=570). All fish for which tagging data were available (n=816) were initially included in analyses even if the data were highly improbable, as with measurements indicating shrinkage between 100 and 350 mm (Fig. 3A).

Growth estimates were obtained from the tagging data by using the maximum-likelihood method and the computer program GROTAG (Francis, 1988b). The growth model fitted was Francis's (1995) mark-recapture analog of Schnute's (1981) size-at-age model (Table 1). This model provides estimates of g_1 and g_2, the mean annual growth of fish of lengths y_1 and y_2 respectively, where y_1 and y_2 are chosen to span the range of lengths at tagging. A simple three-parameter model was initially fitted and then additional parameters (growth variability, seasonal growth variation, measurement error, and curvature in the model) were added in a stepwise manner by selecting the parameter that gave the greatest increase in log likelihood. At each step, likelihood ratio tests were used to determine whether addition of parameters resulted in significantly better fits (Francis, 1988b). Better estimates of the growth parameters can be obtained if measurement error is known (Francis, 1995). There was no way of estimating measurement error without using the current data set; therefore, measurement error was not fixed and this may have compromised estimates of growth. After fitting of the growth model, plots of residuals against length at tagging, time at liberty and expected growth increment were examined for any possible lack of fit of the model.

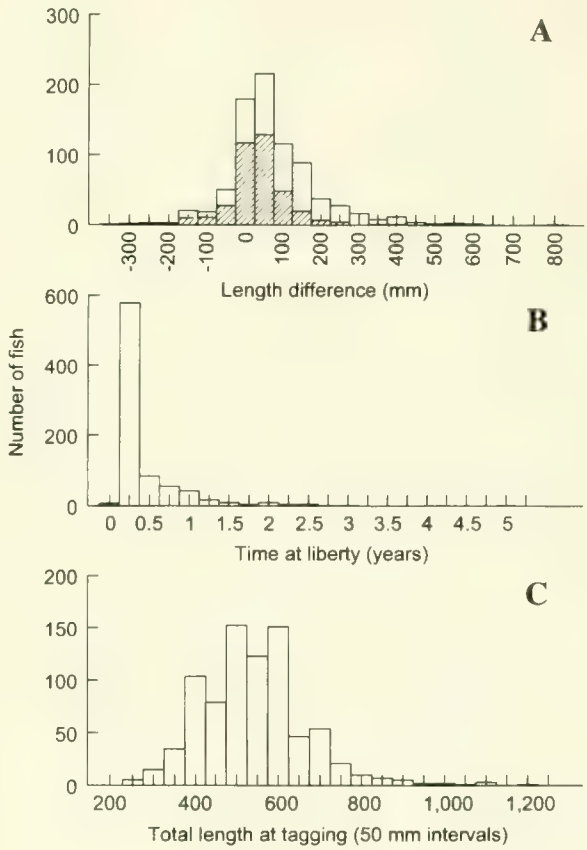

Figure 3

Distribution of (**A**) differences in length between tagging and recapture, (**B**) time at liberty and (**C**) length-at-tagging for kingfish (n=816). Fish recaptured within 30 days are also indicated in A with shading (n=384). Time at liberty (B) includes a small number of fish recaptured the same day that they were tagged (time at liberty=0).

Estimation of rates of growth from length-frequency data

Length-frequency data were obtained from fish sold at the Sydney Fish Markets between November 1985 and December 1989, prior to the introduction of a size limit of 600 mm TL in February 1990. Data were collected haphazardly amongst months and at locations ranging from 30°S to 37°S. Fork length of fish was measured to the nearest 10 mm and the sampling date and fishing area were recorded. Measurements of approximately 16,000 fish were made, enabling stratification of samples by month but not by year or area.

The von Bertalanffy (VB) model was fitted to the time series of 12 monthly length-frequency distributions by using MULTIFAN software (Fournier et al., 1990, 1991). Likelihood-based methods were used to simultaneously analyze the length-frequency distri-

butions sampled at different times to estimate the number of cohorts in the population, the growth parameters (asymptotic length [L_∞] and growth coefficient [K] of the von Bertalanffy growth equation), the age of the first cohort (assuming that the VB curve passes through the origin) and the proportions at age. The simplest model assumes that mean lengths-at-age lie on the VB growth curve and that the standard deviations of length-at-age are identical for all cohorts. More complex models were also tested that allowed 1) sampling bias for the first cohort, 2) age-dependent standard deviation in length-at-age, and 3) seasonally oscillating growth to be added as additional parameters in the model. The more complex models incorporated all possible combinations of these parameters and used likelihood ratio tests to identify the model of best fit. The significance of improvement of fit within models by adding year classes was tested for significance at the 0.10 level (see Fournier et al., 1990), and significance of improvement of fit between models by adding extra parameters was tested at the 0.05 level.

The seasonal form of the von Bertalanffy equation for the length-frequency data is

$$\mu_{ja} = m_1 + (m_N - m_1)\frac{1-\rho^{|(j-1)-(t_a-12)\cdot f(t_a)|}}{1-\rho^{(N-1)}},$$

where $f(t_a) = \frac{\phi_1}{2\pi}\sin\left[2\pi\left(\frac{t_a+1}{12}-\phi_2\right)\right]$,

μ_{ja} = the mean length of fish of the j^{th} age class in the a^{th} length-frequency data set;
m_1 = the mean length of the first age class;
m_N = the mean length of the last age class;
ρ = the Brody growth coefficient;
t_a = the number of months after the presumed birth month of the fish in the a^{th} length-frequency data set;
N = the number of age classes present; and
ϕ_1 and ϕ_2 describe the amplitude and phase of the seasonal component, respectively (Fournier et al., 1990, 1991; Francis and Francis, 1992).

Comparisons of rates of growth from calcified structures and from tagging and length-frequency data

Rates of growth were estimated from aging structures and from length-frequency (both age-based) and mark-recapture (length-based) data with methods outlined in Francis (1995). The aging error model of Richards et al. (1992) that showed the best fit to the data matrix comprising two age readings from each of the three aging structures was used to determine a single age for each fish. Schnute's growth curve (case 2) was then fitted to the age-size data and this mean age-size relationship was used as a basis with which to compare the estimates of growth from the different data sets. The annual growth for the age-size data and length-frequency data was calculated as the mean size at age x minus the mean size-at-age $(x+1)$; Francis, 1995). Annual growth at corresponding points on the size-based line was then estimated at the size the fish was at age x, as determined from the fit to the mark-recapture data obtained by using GROTAG.

Results

Structures for aging *Seriola lalandi* were collected from a total of 572 fish ranging in size from 323 to 1090 mm FL, although not all structures were collected from all fish. Although *S. lalandi* is reported to reach a total length of almost 2000 mm (1700 mm FL) and a weight of 60 kg, fish of this size are rare. In New South Wales, few fish over 20 kg (about 1200 mm FL) are caught by commercial fishermen and the largest fish recorded in surveys of amateur fishermen has been 1140 mm FL (Steffe et al.[2]). We were unable to obtain fish larger than 1100 mm FL.

All structures showed zones that could be interpreted as annuli (Fig. 1); however, zones were not interpretable in all fish. Growth zones in whole otoliths were more easily interpretable than those in sectioned otoliths (Fig. 2); the latter showed numerous striations that could rarely be interpreted. Zones in sectioned otoliths were, however, clearer in some larger fish (Fig. 2). A large number of scales had to be collected because preliminary results showed that two-thirds of fish had at least some regenerated scales. Vertebrae did not always stain well and showed pronounced ridges which reduced readability in many fish.

Validation of aging methods

Analysis of marginal increments showed different patterns among structures (Table 2). Otoliths and scales revealed that one zone was laid down per year, in August–September (otoliths) and between Decem-

[2] Steffe, A., J. Murphy, D. Chapman, B. E. Tarlington, G. N. G. Gordon, and A. Grinberg. 1996. An assessment of the impact of offshore recreational fishing in New South Wales on the management of commercial fisheries. Final Report to Fisherires Research Development Corporation, PO Box 222, Deakin West ACT 2600, Australia.

Table 2

Results of analyses of marginal increments for kingfish aged by otoliths, scales, and vertebrae. Each category is the growth of the structure, subsequent to the most recent zone, as a percentage of the previously completed zone. The percentage of fish in each category for each two-month period is shown; sample sizes are also indicated (in parentheses beside month). Only fish aged 2–4 were used for analyses. For each row, the highest percentage of fish is shown in bold.

	Category				
Month	Edge	20	40	60	80
Otoliths					
Aug–Sep (34)	**44**	35	15	0	6
Oct–Nov (149)	16	**36**	24	10	13
Dec–Jan (87)	9	7	18	24	**41**
Feb–Mar (68)	1	13	**31**	24	**31**
Scales					
Aug–Sep (0)					
Oct–Nov (181)	15	12	21	24	**29**
Dec–Jan (94)	22	**34**	21	7	15
Feb–Mar (101)	1	19	28	**34**	19
Vertebrae					
Aug–Sep (51)	8	16	16	10	**51**
Oct–Nov (173)	16	20	**24**	16	23
Dec–Jan (50)	14	12	**28**	20	26
Feb–Mar (70)	14	13	**37**	11	24

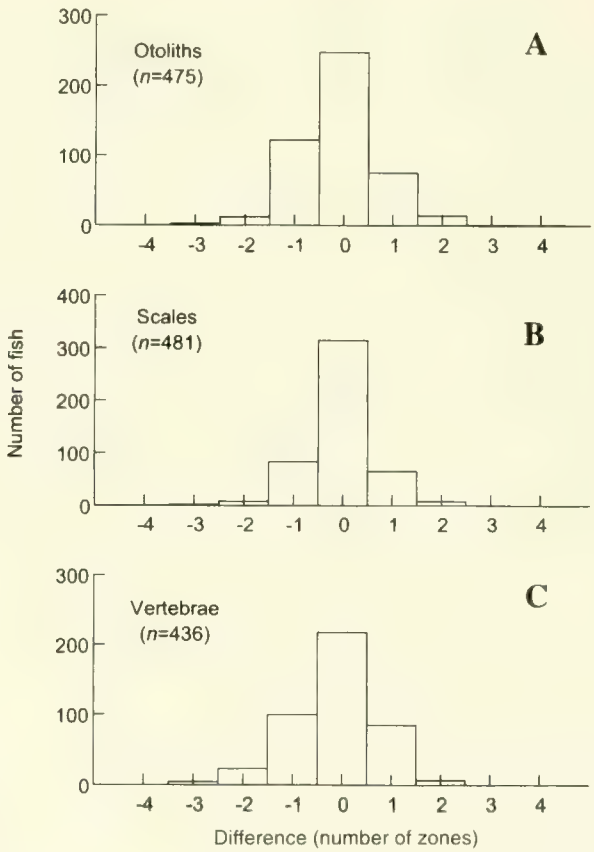

Figure 4

Differences between repeated counts of zones for three structures used to age kingfish. Each comparison represents independent counts from a single reader.

ber and January (scales; Table 2). No data were, however, obtained for scales in August–September and sample sizes were small between April and July (n=1–7 fish per month) for all structures. No clear pattern of marginal zones was observed in vertebrae (Table 2).

Precision within and among structures

Comparisons of two independent counts of zones in a structure resulted in a relatively low level of agreement (50–66%). Depending on the structure, between 92% and 96% of readings agreed within one zone (Fig. 4). Differences in counts of zones varied by up to four zones (Fig. 4). Mean coefficients of variation among counts ranged from 7.6% (scales) to 12% (otoliths).

Comparison of readings between structures showed a large amount of variation, with differences between structures varying by up to six growth zones (Fig. 5). Agreement between any two methods decreased with age, but otoliths and vertebrae had the greatest concordance in fish aged 4 and over. Fish were never assigned an age of 0 when aged with scales; fish assigned 0 or 1 with other structures were assigned an age of 1 with scales. Readings between structures agreed within one zone between 88% (between vertebrae and otoliths) and 91% (between scales and otoliths) of the time.

Estimates of aging error

Analysis of aging precision with the methods of Richards et al. (1992) showed that the estimates of assigned age were more precise for young fish (Fig. 6A). For example, with otoliths, 98% of fish with an estimated most probable age of 0 were likely to be aged as 0, whereas only 74% of fish with a most probable age of 4 were likely to be aged as 4. This precision can be compared with those obtained from other structures (e.g. scales and vertebrae; Fig. 6A). Fish aged with scales had a higher probability of being consistently assigned ages 1 and 2. Fish aged with vertebrae or otoliths, however, had a higher probability of being consistently assigned age 4, whereas there was little difference between the three structures in assigning fish to age 3 (Fig. 6A).

A more complex aging error model, with parameters that accounted for effects due to aging structures showed that fish in their first year (i.e. 0 growth zones) were likely to be overestimated with scales and vertebrae than with otoliths. Otoliths underestimated the age of fish in their first year, although this is due to the relative nature of the model because vertebrae and scales overestimated the age of these fish (Fig. 6B). Scales showed less bias in relation to the other structures for fish aged 1–4 (Fig. 6B).

Estimates of rates of growth

Patterns in growth of kingfish from NSW were obtained from Schnute's (1981) growth model fitted to the estimated most probable ages of fish calculated from the different aging structures (Fig. 7). Size-age data were best fitted by three-parameter models for otoliths, vertebrae (both case 2, see Table 1) and scales (case 3). Using the best fitting model for each structure, we estimated that the average lengths (± standard error) of fish with one growth zone were 499 (±5), 418 (±9), and 485 (±7) mm FL for otoliths, scales, and vertebrae respectively. At age 5, fish were 807 (±8), 823 (±8), and 788 (±6) mm FL for otoliths, scales, and vertebrae respectively. The maximum age of fish was 9 yr for otoliths and scales, compared to 11 yr for vertebrae (Fig. 7). Vertebrae tended to produce higher age estimates than did otoliths and scales, with 5% of fish showing greater than five growth zones in vertebrae compared with only 2% for scales and otoliths. Using a single age for each fish, we estimated an age-length key for fish sampled during the current study (Table 3). Fish in all length classes were found in more than one age class (Table 3).

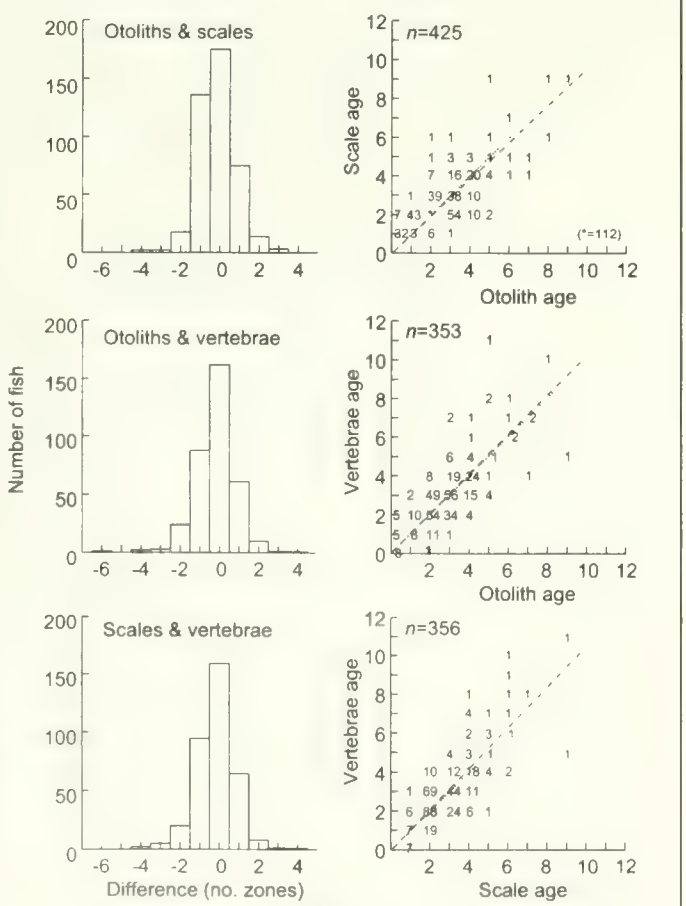

Figure 5

Counts of zones from kingfish otoliths, scales, and vertebrae compared with other aging structures. Histograms show the difference between structures, and the scatterplots enable comparisons between structures by age. In each scatterplot, the line of slope 1 (dotted line) indicates 100% agreement. The line of best fit (dashed line) is indicated with a dashed line. The sample size for each point on the scatterplots is also shown.

The different aging structures showed significant differences in mean size-at-age for some age classes. Scales showed significantly different mean size-at-age to otoliths and vertebrae for fish with one growth zone (t-tests, $P<0.05$). Otoliths and vertebrae gave similar estimates of mean size-at-age for fish with less than eight growth zones (t-tests, $P<0.05$). With the exception of fish with one growth zone, scales gave similar estimates of mean size-at-age to otoliths for all other age classes (t-tests, $P<0.05$). Although differences between scales and vertebrae were statistically significant for some age classes (fish with 4–6 growth zones), these differences were not likely to be biologically important.

Kingfish that were measured at both tagging and recapture were at large for between 0 days (i.e. recaptured the same day that they were tagged) and 5 years (Fig. 3B). Growth of recaptured fish ranged from a decrease of 350 mm to an increase of 800 mm (Fig. 3A). The frequency distribution of fish at large <30 days showed that fishermen were just as likely to underestimate the length of fish as they were to overestimate the length of fish (Fig. 3A). The mean difference in size of fish between tagging and recapture for fish recaptured within 30 days was 11.6 mm (±0.4, SE), suggesting that there was little bias in measurements between tagging and recapture. Size of fish at tagging ranged from 220 to 1200 mm, although the majority of fish were between 400 and 600 mm TL (Fig. 3C).

The best fit to the complete tag-recapture data set (model 1 in Table 4) showed a high proportion of outliers ($P=0.04$). Twenty-two fish (or 2.7%) that had absolute standardized residu-

als greater than 3 in the model 1 fit were removed from the data set. Initially, a simple three-parameter model was fitted (model 2 in Table 4), which indicated growth rates of 255 mm and 176 mm for 400-mm and 600-mm fish, respectively. The first additional parameter selected was that describing the shape of the growth curve (model 3 in Table 4). Model 3 showed annual growth rates of 270 and 140 mm. There was a significant improvement in fit when a term describing growth variability was added (model 4 in Table 4). Additional parameters (e.g. seasonal growth terms) did not result in significant improvements of fit. The best fitting model was therefore case-1 model in Table 1. Plots of standardized residuals against length at tagging, time at liberty, and expected growth increment showed no pattern (correlations were 0.022, 0.003, and 0.005, respectively) suggesting that the model was appropriate.

The best fitting model for the kingfish length-frequency data set identified five cohorts aged from 1.73 to 5.73 years (Table 5; Fig. 8). The standard deviation of the predicted length estimates for each age class increased with age. Parameters for first length bias and seasonal growth were also included in the best fitting model (Table 5; Fig. 9). Estimates of the mean length-at-age (and standard deviation) for the length-frequency data set are given in Table 5. The mean lengths and proportions of the modes predicted by MULTIFAN generally fitted the observed data (Fig. 8). There were large numbers of small fish (e.g. 1 yr) in the catch during the summer months (e.g. November and December), whereas 2-yr fish dominated the catch at other times. Small numbers of large fish (e.g. greater than 5 yr) were found throughout the year (Fig. 8). The seasonal form of the von Bertalanffy growth equation showed that the projected value of L_∞ was 1252 mm FL and the rate of change in growth increment (K) was 0.189 (Fig. 9).

Comparison of annual growth between age-based (age-length and length-frequency) and length-based (mark-recapture) data, although not strictly comparable, showed a decrease in growth with age and size of fish (Fig. 10). Estimates of annual growth were similar among the three methods for 2–4 year fish (≈550–750 mm SL) but varied by ≈50 mm for 1-yr-old fish.

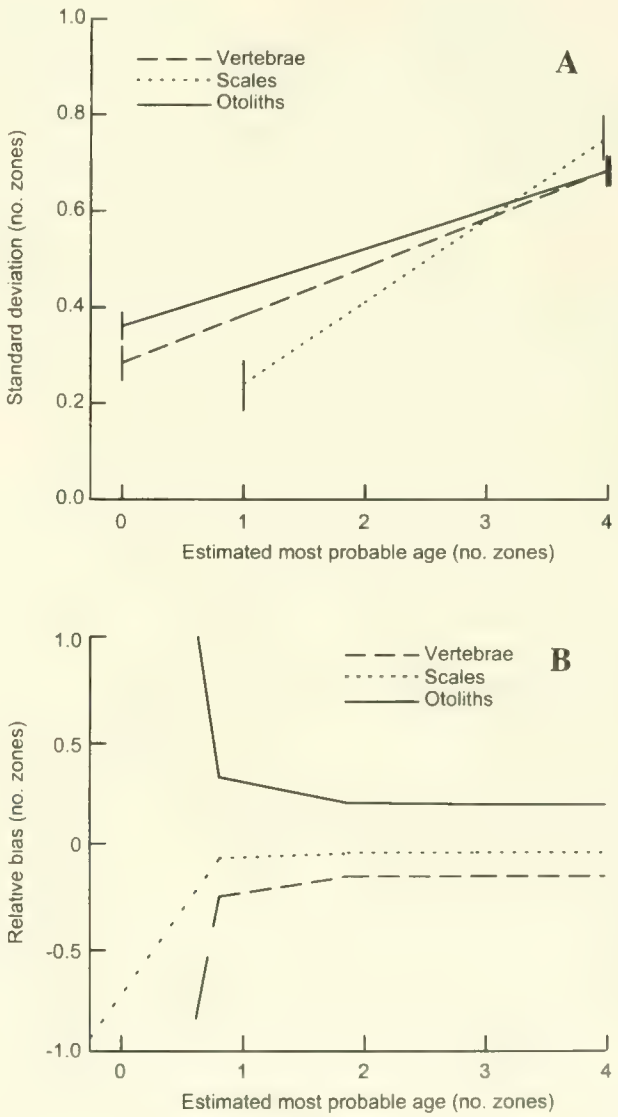

Figure 6

(**A**) Aging error versus estimated most probable age for kingfish aged with otoliths, scales, and vertebrae. Estimated most probable age was calculated separately for each structure by using the methods of Richards et al. (1992), see text for further details. Errors around the first and last ages are indicated by the vertical lines. (**B**) Relative bias versus estimated most probable age for kingfish aged by otoliths, scales, and vertebrae. Relative bias was calculated from a model that incorporated two age readings from each of the three structures.

Discussion

All structures showed patterns of growth that were, to varying degrees, quantifiable. Delineation of each zone was, however, sometimes difficult, as has been found in other studies (e.g. Brennan and Cailliet, 1989; Manooch and Potts, 1997), and the clarity of zones varied among individuals for all structures. Because pelagic fishes including *Seriola* spp. are known to be difficult to age, these results were not surprising.

To accurately reflect the age of a fish, the zones must be formed on a regular and determinable time scale.

Small sample sizes during the winter months (from April to July), due in part to small numbers of fish being taken in the fishery, made analysis of marginal increments problematic, especially for scales because samples were also not obtained in August–September. With the exceptions of otoliths and possibly scales, our data were not sufficient to confirm that only one zone was formed per year. No single category of marginal growth ever had more than 50% of fish for any structure. A previous study (Mitani and Sato, 1959) also found that fish (*Seriola quinqueradiata*) collected in any one time period showed a wide range of marginal growth conditions. Growth zones on the edge of the otoliths of *S. dumerili* were also found over five months of the year (Manooch and Potts, 1997). The wide range of marginal growth patterns in our study may in part be due to grouping of samples into two-month intervals or because fish from three age classes (2–4 growth zones) were used in analyses. Fish from different age classes have previously been shown to lay down zones at slightly different times of year (e.g. Francis et al., 1992).

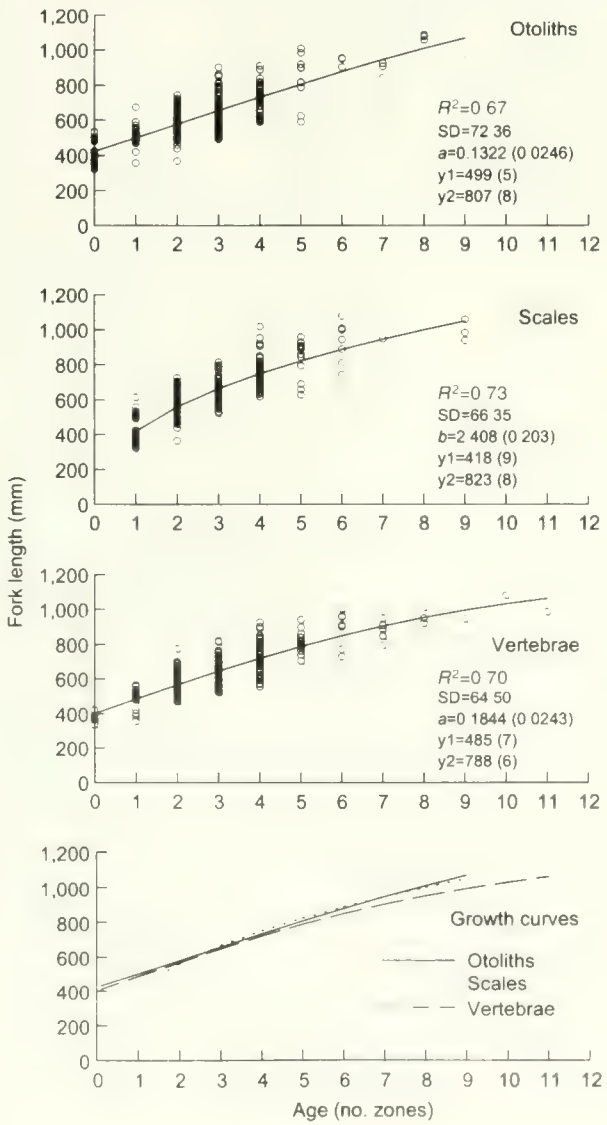

Figure 7

Relationship between fork length and age for the different structures used to age kingfish (**A–C**) and (**D**) comparison of the three growth curves. The growth curves were calculated by using Schnute's growth model. R^2, overall standard deviation (SD), and the parameters (standard error) describing the growth model are shown. y_1 is size at age 1, y_2 is size at age 5, a and b are parameters that describe the shape of the curve. The formulae for the growth curves are found in Table 1.

Analysis of marginal increments often provides only partial validation of age estimates because older fish with slower growth often do not show seasonality in formation of zones. A method should not be considered accurate until all reported ages are validated (Beamish and McFarlane, 1983). Validation of age estimates in older fish will require a mark-recapture study, but further work on validation in younger fish may use a variety of approaches (e.g. length-frequency analyses if cohorts are easily recognized, mark-recapture etc). In the present study, few tagged fish were at large more than a year (Fig. 3B), which suggests that many fish would have to be tagged in a mark-recapture study to recover sufficient fish to make this approach feasible.

There have been few validation studies on *Seriola* spp. and all have involved analysis of marginal increments. Mitani and Sato (1959) have suggested that one zone is laid down each winter in opercular bones of *S. quinqueradiata* and Baxter (1960) found that zones are formed between November and January in scales of *S. lalandi* (formerly *dorsalis*). In otoliths of *S. lalandi* opaque zones appear to be laid down in August or September. Timing of zone formation in scales and vertebrae was more variable and may differ between structures because processes involved in deposition vary among bone, scales, and otoliths (Simkiss, 1974).

Precision of aging estimates

Exact agreement among age estimates for each structure was generally poor; agreement within one zone was reasonable for all structures. The use of percent agreement (i.e. percent of fish aged alike between sets of multiple readings) has been criticized because it fails to take into account the range of year classes of fish and therefore can be used only for age-specific comparisons (Kimura

Table 3

Kingfish age-length (FL, mm) distribution for fish collected from New South Wales, Australia, between August 1995 and July 1996. Shown are the number of fish and the percentage of the length class (in parentheses). Ages were estimated from the aging error model that showed the best fit to the data matrix comprising two age readings from each of the three aging structures where fish had less than five growth zones or by randomly selecting one of the six age readings where fish had five or more growth zones.

	Age (yr)										
Length class	0	1	2	3	4	5	6	7	8	9	Total
300–350	4 (66.7)	1 (16.7)	1 (16.7)								6
351–400	11 (47.8)	7 (30.4)	5 (21.7)								23
401–450	4 (40.0)	4 (40.0)	2 (20.0)								10
451–500		11 (34.4)	19 (59.4)	2 (6.3)							32
501–550		11 (10.6)	85 (81.7)	8 (7.7)							104
551–600		1 (1.1)	67 (71.3)	26 (27.7)							94
601–650			54 (50.9)	51 (48.1)	1 (0.9)						106
651–700			14 (19.2)	52 (71.2)	6 (8.2)	1 (1.4)					73
701–750			5 (13.2)	16 (42.1)	14 (36.8)	2 (5.3)	1 (2.6)				38
751–800			1 (3.1)	9 (28.1)	16 (50.0)	4 (12.5)	1 (3.1)	1 (3.1)			32
801–850				3 (21.4)	4 (28.6)	4 (28.6)	3 (21.4)				14
851–900					2 (62.5)	5 (62.5)	1 (12.5)				8
901–950					1 (18.2)	2 (18.2)	4 (36.4)	3 (27.3)		1 (9.1)	11
951–1000							1 (33.3)		1 (33.3)	1 (33.3)	3
1001–1050						1 (33.3)	1 (33.3)		1 (33.3)		3
1051–1100									1 (33.3)	2 (66.7)	3
N	19	35	253	167	44	19	12	4	3	4	560

Table 4

Log likelihood function values, growth parameter estimates, and standard errors (model 4 only) for kingfish (*Seriola lalandi*) tagging data. * indicates that parameters were held fixed. Standard errors of parameter estimates were estimated from simulated data (n=100 simulations). Growth rates are shown for 400 mm (g_{400}) and 600 mm (g_{600}) TL fish. The best model fit (model 4) is the case-1 model from Table 1.

Parameter		Model 1	Model 2	Model 3	Model 4	SE
Log-likelihood		2890.67	2797.80	2735.35	2706.21	
Mean growth rate	g_{400} (mm)	263.8	255.3	269.6	260.3	8.1
	g_{600} (mm)	132.1	176.4	140.1	131.1	7.3
Seasonal variation	u (year)	0.164	0*	0*	0*	
	w (year)	0.706	0*	0*	0*	
Growth variability	v	0.397	0*	0*	0.40	0.045
SD measurement error	s (mm)	66.9	82.1	75.8	66.4	1.70
Outlier contamination	P	0.037	0*	0*	0.000	
Curvature in model	b	5.47	0*	5.21	5.66	0.568
Sample size	n	816	794	794	794	

and Lyons, 1991). More recently, the belief that percentage agreement is inappropriate has been questioned. Although it is acknowledged that percent agreement is not interpretable as a property of the species or stock, it is thought to be more intuitive than other methods (Hoenig et al., 1995). Coefficient of variation (CV) is thought to adjust for the absolute age of the fish and therefore is frequently used to make comparisons among species of varying ages. Kingfish had values of CV within those of previous studies, but at the higher end (present study 7.6–12% versus other species 3.2-12.9% [Kimura and

Lyons, 1991]) suggesting that *S. lalandi* was a more difficult species to age. For kingfish, scales (7.6%) had lower values of CV than did otoliths (12%) and vertebrae (11%). The lowest CV values were for structures where no fish were in their first year (e.g. scales), and the highest values were for structures where fish were aged as in their first year (e.g. otoliths and vertebrae). Similarly, Kimura and Lyons (1991) found that the CV was highest for species in which 1-year age classes were present and lowest where the youngest age classes were 2 or 3 years. Coefficient of variation therefore depends on the minimum age of fish and we suggest that its use be limited to comparisons where fish have the same range of ages. Such indices, if averaged over all fish, are also thought to simplify the data because any trends that might occur with age are ignored (see Hoenig et al., 1995). Precision of aging decreased with age of fish for all structures, suggesting that estimates of precision should not be averaged over all age classes. We believe that the methods of Richards et al. (1992) give a better indication of aging error, and therefore precision, than did methods that summarized over all age classes.

Length at age

Estimates of mean size-at-age calculated from growth models suggested that the resulting growth curves from otoliths, scales, and vertebrae were similar for all but the youngest age class. Although other aging studies on *Seriola* spp. have calculated average length-at-age (e.g. Mitani, 1955; Mitani and Sato, 1959), few have fitted models to the data (but see Baxter, 1960; Manooch and Potts, 1997). Growth models from all aging structures were within the range of growth of *Seriola* spp. described elsewhere (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959; Baxter, 1960; Murayama, 1992).

Further research needs to focus on the position of the first zone in all structures because this may contribute to differences in the shape of the growth curves between structures. No fish were found to be in their first year (i.e. 0) when aged with scales, but fish were found to be in their first year when aged with otoliths and vertebrae. There are also differences in estimated mean size between scales and both otoliths and vertebrae for fish with one growth zone, which is also likely to be due to the detectability of the first zone. Either scales lay down a false first zone or the first zone is not detected in otoliths and vertebrae, possibly because it is close to the edge of the structure. Collections of fish from recruitment over a 12-month period and sampling of all structures may help elucidate the position of the first zone.

Table 5

Estimated parameters from the MULTIFAN analysis of the length-frequency data, with predicted fork lengths (FL) and standard deviations (SD) of lengths at age.

Parameter	Estimated value
Number of cohorts (N)	5
von Bertalanffy K	0.189/year
von Bertalanffy L_∞	1,252 mm
Brody's rho (ρ)	0.828
First length (m_1)	349.5 mm
Last length (m_N)	828.4 mm
Age of first year class	1.73 years
Mean length sampling bias	26.13 mm
Seasonal growth amplitude (ϕ_1)	0.611
Seasonal growth phase (ϕ_2)	0.087 years
Mean SD	44.4 mm
Ratio of first to last SD	1.897

Age	Predicted FL (mm)	Length-at-age SD
1	349.5	32.2
2	505.0	39.7
3	633.7	47.1
4	740.2	54.3
5	828.4	61.1

Although, it is well known that age estimates from scales are inaccurate once growth becomes asymptotic (Beamish and McFarlane, 1987), scales did not appear to underestimate ages of kingfish in relation to otoliths in the present study but may have underestimated ages of older fish in relation to vertebrae (e.g. Fig. 5). In a previous study on *S. lalandi*, spaces between circuli became increasingly narrow after the seventh year, so that it was impossible to differentiate between one year's growth and the next (Baxter, 1960). Few fish, however, had greater than seven growth zones in the current study.

Many studies have found that sectioned otoliths are preferable to whole otoliths for aging because examination of whole otoliths does not take into account the asymmetric deposition of material (Campana, 1984). After a certain age, deposition may thicken the otolith and growth along the anteroposterior axis may decline; therefore only transverse sections would reveal recently formed growth zones (Beamish, 1979). Growth zones on whole otoliths were interpretable for aging kingfish, but zones could rarely be interpreted on sectioned otoliths. This is unusual because in many studies, sectioned otoliths have been found to give more precise and accurate estimates of age than whole otoliths (e.g. Beamish,

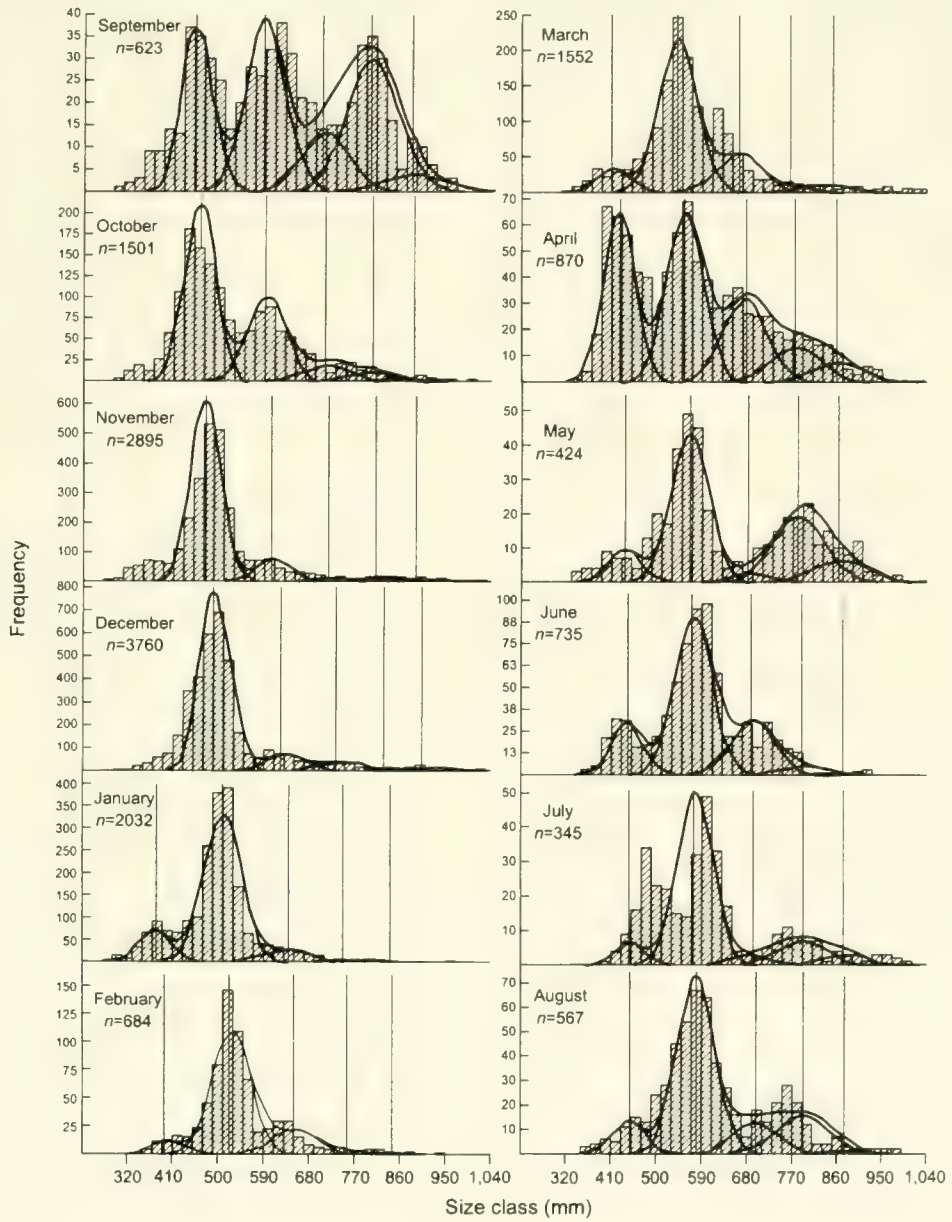

Figure 8

Observed length-frequency distributions for kingfish data (shaded histograms), showing the fit of the MULTIFAN model (see Table 5 for model details). Estimated frequencies for each age class (inner smoothed curves) and for the sum of all age classes (outer smooth curve) are shown. Vertical lines represent the estimated mean lengths-at-age in each sample.

1979; Campana, 1984). Manooch and Potts (1997) have used sectioned otoliths to age *S. dumerili* but commented that age and growth determinations were very difficult. Measurements could only be made on 48% of samples and zones could only be counted on 71% of samples and thus may have biased estimates of growth in their study. Whole otoliths were examined in their study solely to determine the plane of sectioning (Manooch and Potts, 1997). Because whole otoliths may underestimate age of large fish (e.g. Beamish, 1979; Campana, 1984), it may also be useful to look at transverse sections of otoliths of kingfish for extremely large fish (>20 kg).

Comparison of age- and length-based data

Although not strictly comparable (see Francis, 1988a, 1995), estimates of growth from length-frequency,

age-length (both age-based data), and tagging data (length-based) showed agreement for fish aged 2–4 years but varied for fish with one growth zone. Differences in rates of growth were greater for younger fish than for older fish and may have been caused by inaccuracies in aging, influence of tagging on growth (e.g. McFarlane and Beamish, 1990), within- or between-year differences, and variations in year-class strength. Although estimates of growth from tagging data provide some indication that age-length data may be reasonable, they should not be used as a means of validation (see Francis, 1988a).

Tagging data also suggest that *S. lalandi* in New South Wales has greater annual growth than the same species in New Zealand and the United States (Baxter, 1960; Holdsworth[3]). For *S. lalandi* in New South Wales, annual growth rates of 144 mm were found for 500-mm-FL fish, compared with 93 mm (New Zealand) and a range of 34–109 mm (US) for similar size fish. In New Zealand, annual growth of 44 mm was found for 1000-mm-FL fish, which is within the range found in the United States (19–70 mm). Few large fish were tagged in New South Wales, preventing estimates of annual growth at this larger size.

Figure 9

MULTIFAN growth curve for the length-frequency data. A model incorporating seasonal growth is shown. Values of t_0, K, and L_∞ (mm) are shown.

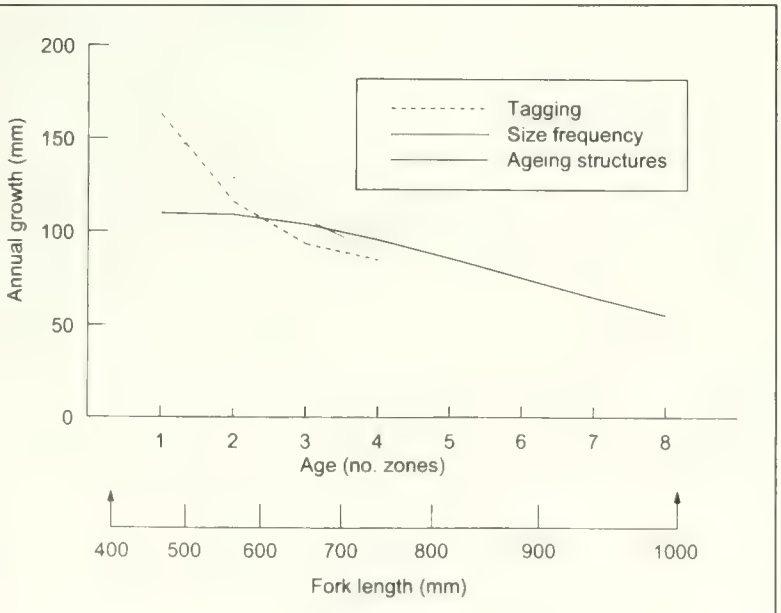

Figure 10

Comparison of rates of annual growth for kingfish estimated from (**A**) aging structures, (**B**) length-frequency (both age-based) and (**C**) mark-recapture (length-based) data. The mean length at any age is aligned with the corresponding point on the age axis; this was calculated from age-size data obtained from the aging structures.

Practicalities of aging kingfish

With the exception of dorsal spines, which did not appear useful for aging kingfish, only scales can be easily collected without altering the market value of the fish because *Seriola lalandi* are preferentially sold whole in NSW. Scales showed similar estimates of mean size-at-age to otoliths for all age classes except fish with one growth zone, but their use in aging kingfish can only be recommended with caution until the position of the first growth zone is better understood. The usefulness of otoliths and vertebrae may be limited by the cost of fish, but, if possible, collections of at least one of these structures should be made. The similarity of age estimates among structures suggests that, if validations are possible, kingfish may be aged reliably.

Acknowledgments

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[3] Holdsworth, J. C. 1997. Ministry of Fisheries, 17 Keyte Street, Kensington, private Bag 9013, Whangarei, New Zealand. Unpubl. data.

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Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico

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Abstract.—Fishing pressure on vermilion snapper, *Rhomboplites aurorubens*, in the Gulf of Mexico has increased since the mid-1970s, and populations are thought to be overfished. We sampled 858 vermilion snapper (192–585 mm TL) from the eastern Gulf of Mexico during 1995 and 1996 to assess their age structure, growth, mortality, spawning season, size and age at maturity, and batch fecundity. The lengths of males and females in our samples were not significantly different, and the overall sex ratio was not significantly different from 1:1. Marginal-increment analysis indicated that one opaque zone is formed on vermilion snapper otoliths during the late spring to early summer of each year. Ages ranged from 1 to 13 years, and von Bertalanffy growth models for males and females were not significantly different. Von Bertalanffy growth model parameters were L_∞ = 298 mm TL, K=0.25/yr, and t_0=–3.9 years for all aged fish. Growth rates in our study were lower than those in previous studies of Gulf of Mexico vermilion snapper, perhaps the result of recent changes in fishing selectivity. Pooled estimates of total instantaneous mortality were 0.480/yr based on recreational landings data and 0.489/yr based on commercial landings data. Most females and all males examined were mature. At 200 mm TL, 90% of the females we examined were mature. Vermilion snapper are summer spawners, and ripe females were caught from May to September. Batch fecundity ranged from 5535 to 22,811 oocytes and was positively correlated with fish weight (batch fecundity=317 × (whole weight) – 3.1624×10^4, $r^2 = 0.55$).

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Fish. Bull. 97:828–841 (1999).

The vermilion snapper, *Rhomboplites aurorubens*, is a small, subtropical lutjanid that occurs from North Carolina to Rio de Janeiro but is most abundant off the southeastern United States and in the Gulf of Campeche (Vergara, 1978). In the Gulf of Mexico (GOM), vermilion snapper are usually found near hard bottom areas off the west-central Florida coast, the Florida Middle Ground, and the Texas Flower Gardens (Smith et al., 1975; Smith, 1976; Nelson, 1988). Faunal surveys in the South Atlantic Bight (SAB) have indicated that vermilion snapper are most common over inshore live-bottom habitats and over shelf-edge, rocky-rubble, and rock-outcrop habitats (Grimes et al., 1977, 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984).

Vermilion snapper are an important component of the reef fish fishery on the west coast of Florida. In 1995 and 1996, total commercial landings of vermilion snapper on Florida's west coast was 1.6 million pounds and had an estimated dockside value of $4.5 million (Marine Fisheries Information System[1]). Over the same period, 1.8 million vermilion snapper were landed by anglers in Florida (MRFSS[2]). Charter boats or headboats accounted for most (90%) of the angler-caught fish (Goodyear and Schirripa[3]; Schirripa[4]).

The Gulf of Mexico stock of vermilion snapper is showing signs of being overfished. Schirripa[4] reported in an analysis of GOM vermilion snapper landings data that 1) overall landings were declining, 2) the fishery was consolidating to the most productive fishing areas, 3) the mean size of fish in the commercial catch was decreasing, 4) the catch per unit of effort was decreas-

[1] Marine Fisheries Information System. 1997. Florida Department of Environmental Protection, 100 8th Avenue S.E., St. Petersburg, FL. Unpubl. data.

[2] MRFSS (Marine Recreational Fishery Statistics Survey). 1997. Fisheries Statistics Division, National Marine Fisheries Service, Department of Commerce, Silver Springs, MD. Unpubl. data.

[3] Goodyear, C. P., and M. J. Schirripa. 1991. A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL. Contribution rep. MIA-90/91-78.

[4] Schirripa, M. J. 1996. Status of the vermilion snapper fishery of the Gulf of Mexico: assessment 3.0. Miami Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL. Contribution rep. MIA-95/96-61.

ing, and 5) the estimated number of age-1 fish in the population was declining. Goodyear and Schirripa[3] also noted that large differences in estimates of length-at-age and estimates of fecundity made it difficult to assess confidently conditions of the stock by using standard assessment models.

Existing age and growth data for this species in the GOM are inadequate and dated. Zastrow (1984) and Nelson (1988) used scales to age GOM vermilion snapper collected in the early 1980s. The maximum age reported was 7 years. However, using scales to determine age has proven to be problematic. Studies in the SAB have shown that as age increases, the readability of the scales decreases (Grimes, 1978; Collins and Pinckney, 1988). Barber (1989) used whole otoliths and scales to age GOM fish and was able to count up to 18 rings in scales and 26 rings in whole otoliths. Although he did not directly compare ages from both structures, his scale- and otolith-based estimates of length at age and growth were very different. In addition, his attempt to validate whole-otolith-based ages was unsuccessful.

Growth of vermilion snapper may be affected by changes in fishing. Zhao et al. (1997) found that mean and predicted sizes-at-age of SAB fish had declined between 1979 and 1993 and associated this change with size-selective fishing. They suggested that fishing is removing faster-growing fish from the population and may have genetic or physiological consequences in the life history of this species.

Information on the reproductive biology of vermilion snapper in the GOM is limited. Sex ratio appears to be dependent on location. Sex ratios from the GOM and Puerto Rico are approximately 1:1 (Boardman and Weiler, 1979; Zastrow, 1984; Collins[5]) although Nelson (1988) reported that males outnumbered females 1.2:1. In the SAB, females consistently outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Collins and Pinckney, 1988; Cuellar et al., 1996; Zhao and McGovern, 1997). Nelson (1988) examined spawning period, fecundity, and sex ratios of fish caught in the western GOM. His results were similar to findings reported for the SAB (Grimes and Huntsman, 1980; Cuellar et al., 1996). In both regions, spawning occurs during the summer and early fall. Nelson (1988) estimated that vermilion snapper batch fecundities in the GOM range from 61,600 to 392,000 eggs. Fecundity has been found to have a positive relationship with fish size (Grimes and Huntsman, 1980; Nelson, 1988; Cuellar et al., 1996). Vermilion snapper are thought to spawn in aggregations. Boardman and Weiler (1979) and Grimes and Huntsman (1980) found large numbers of fish in the same reproductive state in single collections.

Basic life-history information is needed to properly assess vermilion snapper stocks in the GOM. Accurate ages are needed to develop age-length keys, develop growth models, and estimate total mortality. In addition, the annual periodicity of ring deposition in otoliths has not been validated in the GOM. With the increasing reliance on estimates of spawning-potential ratios to describe a stock's condition, information on maturation schedules, sex ratios, and size-specific fecundities are also needed. The purpose of this study was to accurately age eastern GOM vermilion snapper to develop age-length keys, develop growth models, construct catch curves for deriving estimates of total mortality, and to describe the reproductive biology of this species.

Methods

Eastern GOM vermilion snapper were sampled from October 1995 to September 1996. Samples were obtained from headboat fishermen, commercial catches, and a Florida Department of Environmental Protection trawl survey. Total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter. Whole weight or gutted weight (or both) were measured to the nearest gram. The relationships between lengths and $\log_{10}$-transformed total lengths and weights were determined by least-squares regression (SAS Institute, Inc., 1985). Male and female regression lines of $\log_{10}$-transformed total lengths and weights were compared by using analysis of covariance (Snedecor and Cochran, 1971).

Thin sections of sagittae (hereafter referred to generally as otoliths) were used to determine the ages of fish. Otoliths were removed and stored dry in culture wells. The left otolith was serially sectioned across its anterior–posterior midpoint at 0.5-mm intervals by making a transverse cut with an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope. The magnified images of otolith sections were transmitted by means of video camera to a video monitor and were analyzed with a computer-driven data-acquisition software package (Optimas Corp., 1996). The number of opaque zones and the radial measurements from the core to the last opaque band and to the edge of the otolith (otolith radius, Fig. 1) were recorded. Marginal increments were measured as the distance between the last opaque band and the edge of the otolith.

[5] Collins, A. 1997. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., 3500 Delwood Beach Road., Panama City, FL 32407. Personal commun.

To determine the precision of vermilion snapper otolith opaque zone counts, otoliths collected during the first four months of sampling (n=200) were read independently by two investigators. After the first reading, readers examined the sections together and compared counts to form a consensus about what constituted an opaque zone. The two readers then re-examined the sectioned otoliths independently, and counts were compared again. Because agreement between readers was 100%, one reader read the remaining otoliths to determine age. Each of the remaining otolith sections was read three times, and opaque zone counts were accepted for ages only if at least two of the three separate readings were the same. To validate annulus periodicity, marginal increments and their medians were plotted by month for each age and compared for consistent temporal patterns.

Age in years was estimated as the number of opaque zones. Therefore, length at age included any growth that occurred after the last opaque ring was formed. Mean length at age was calculated for males, females, and all aged fish. Age and observed length data were fitted to a von Bertalanffy growth model by using a nonlinear regression (SAS Institute, Inc., 1985). Growth curves were fitted separately for males, females, and all aged fish. The estimated parameters for male and female curves were compared by using likelihood-ratio tests (Kimura, 1980; Cerrato, 1990). We calculated an adjusted r^2 for the resulting curves by using methods described by Helland (1987).

We used age-frequency data from this study to estimate mortality rates from the commercial and recreational length data. Because the numbers of vermilion snapper measured in fishery sampling programs were low, we pooled the most recent years where data were available. Length data from commercial landings were obtained from the TIPS[6] from 1992 to 1994, and in 1996. Length data from recreational landings were obtained from the MRFSS[2] and pooled for years 1990–96. Instantaneous mortality and survivorship were estimated by the Chapman-Robson method (Youngs and Robson, 1978). Age at full recruitment was estimated from the catch curve as the next oldest age from the age with the greatest catch.

Reproductive analyses were based on gonad weights and a histological examination of gonadal tissue. Whole gonads were weighed to the nearest 0.1 g, fixed in 10% buffered formalin for approximately one week, rinsed in water, and then transferred to 70% ethanol. A sample was taken from the middle of the pre-

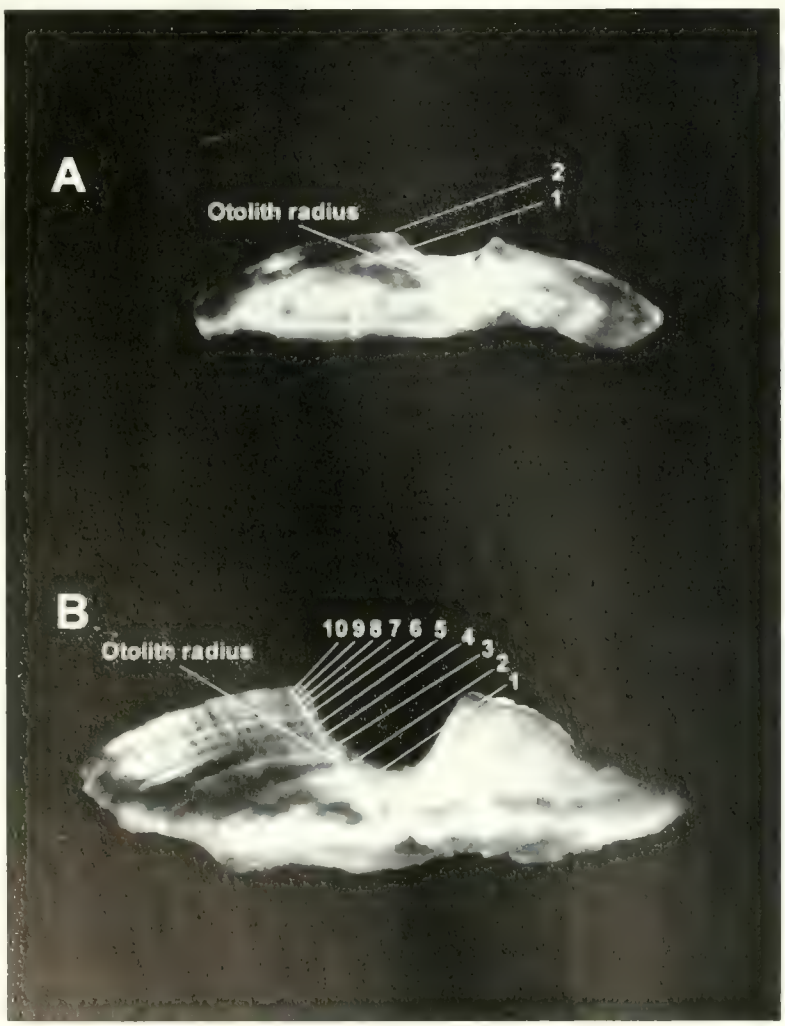

Figure 1

Sectioned saggitae from (**A**) a 2-year-old (204-mm-TL) and (**B**) a 10-year-old (184-m-TL) vermilion snapper. Both fish were caught in the eastern Gulf of Mexico in July 1996.

[6] TIPS (Trip Interview Program). 1997. Florida Department of Environmental Protection, 100 8th Avenue, S. E., St. Petersburg, FL. Unpubl. data.

Table 1
Gonad development classes for vermilion snapper.

Class	Ovary	Testes
Immature	Only primary growth oocytes present.	Spermatogonia and spermatocytes in the central lobules; no tailed sperm in the lumen of the lobule.
Resting	Primary growth oocytes and atretic bodies present.	Mostly spermatogonia and spermatocytes in the central lobules. Free spermatozoa in the lumen of the lobule, and brown bodies (Grier, 1987) may be present.
Early developing	Primary growth and cortical alveoli (yolk vesicle) oocytes present. Atretic bodies may be present.	
Developing	Primary growth, cortical alveoli, and vitellogenic oocytes present.	Mostly spermatocytes and spermatids in the central lobules, free spermatozoa in the lumen of the lobule.
Ripe	Primary growth, cortical alveoli, vitellogenic, and late-stage vitellogenic or hydrated oocytes present. Postovulatory follicles (POFs) may be present.	Mostly spermatozoa found in the central lobules and in the lumen of the lobule.
Spent	Primary growth oocytes present. Possibly some cortical alveoli oocytes present. Vitellogenic oocytes undergoing massive atresia.	Few free spermatozoa in the lumen of the lobule; early stages of spermatogenesis in the peripheral lobules.

served gonad and embedded in paraffin. We cut a 5.0-μm section from the sample, stained it with Harris's haematoxylin, counterstained it with eosin (Humason, 1972), and examined it under a compound microscope to determine sex and gonad developmental state. In addition, the frequency of oocyte developmental stages (including atretic bodies and postovulatory follicles) was tabulated for approximately 300 oocytes from each ovary by using a computer-driven data-acquisition software package (Optimas Corp., 1996). Gonadal development classes (Table 1) were determined by using modified classification schemes developed from West (1990) and Wallace and Selman (1981) for females and from Hyder (1969) for males.

Reproductive seasonality was determined by examining the monthly changes in gonad classes, the monthly distribution of oocyte stages, and the monthly changes in the gonadosomatic index (GSI). The GSI was calculated by the following equation:

$$GSI = gonad\ weight/(whole\ weight - gonad\ weight).$$

If whole weight was not available, it was estimated from TL. Batch fecundity was estimated by counting hydrated oocytes following the gravimetric method described by Hunter et al. (1985). The relation between fish weight and batch fecundity was examined for a significant correlation by means of least-squares regression analysis (SAS Institute, Inc., 1985).

Results

Collections

We sampled 858 vermilion snapper that ranged from 192 to 585 mm TL. Most fish (87%) were between 201 and 325 mm TL. Relationships between lengths, between lengths and weights, and between weights are seen in Table 2. Male and female data were pooled for the weight-length relationship because no significant difference was found between slopes and y-intercepts of sex-specific regression equations (analysis of covariance, P=0.47 and 0.08, respectively). Most fish came from the recreational fishery (n=661) and ranged in length from 192 to 400 mm TL (Fig. 2). Fish from the commercial fishery (n=168) ranged from 225 to 585 mm TL. The mean length of recreationally caught fish (256 mm TL, SE=29) was significantly less than the mean length of commercially caught fish (324 mm TL, SE=90; t-test, P<0.001). The length-frequency distributions for commercially and recreationally caught fish were significantly different (χ^2=216, df=5, P<0.001). Fish obtained from the trawl survey (n=27) were small and ranged in length from 205 to 253 mm TL.

The mean length of males (256 mm TL, SE=4) was not significantly different from that of females (261 mm TL, SE=3; t-test, P=0.315). Males (n=392) ranged in length from 199 to 585 mm TL and females (n=430) from 192 to 518 mm TL (Fig. 2). The overall sex ratio of males to females was 1:1.1 and was not signifi-

Table 2

Linear relationships ($Y=a+bX$) between length and length, length and weight, and weight and weight for vermilion snapper from the eastern Gulf of Mexico. SL is standard length (mm); FL is fork length (mm), TL is total length (mm); WT is whole weight (gm); GWT is gutted weight (gm). n is the number of fish sampled, and standard error is in parentheses.

Y	X	n	a	b	r^2
SL	FL	857	7.5 (0.8)	0.82 (0.003)	0.99
SL	TL	869	10.5 (1.0)	0.72(0.004)	0.98
FL	SL	857	–5.5 (1.1)	1.20 (0.005)	0.99
FL	TL	854	3.4 (0.6)	0.88 (0.002)	0.995
TL	SL	869	–8.4 (1.4)	1.36(0.007)	0.98
TL	FL	854	–2.6 (0.6)	1.13 (0.003)	0.995
WT	GWT	89	–11.8(2.3)	1.15 (0.012)	0.99
$\log_{10}$WT	$\log_{10}$TL	646	–4.60(0.084)	2.87 (0.035)	0.91
$\log_{10}$GWT	$\log_{10}$TL	170	–5.01(0.05)	3.03(0.02)	0.99

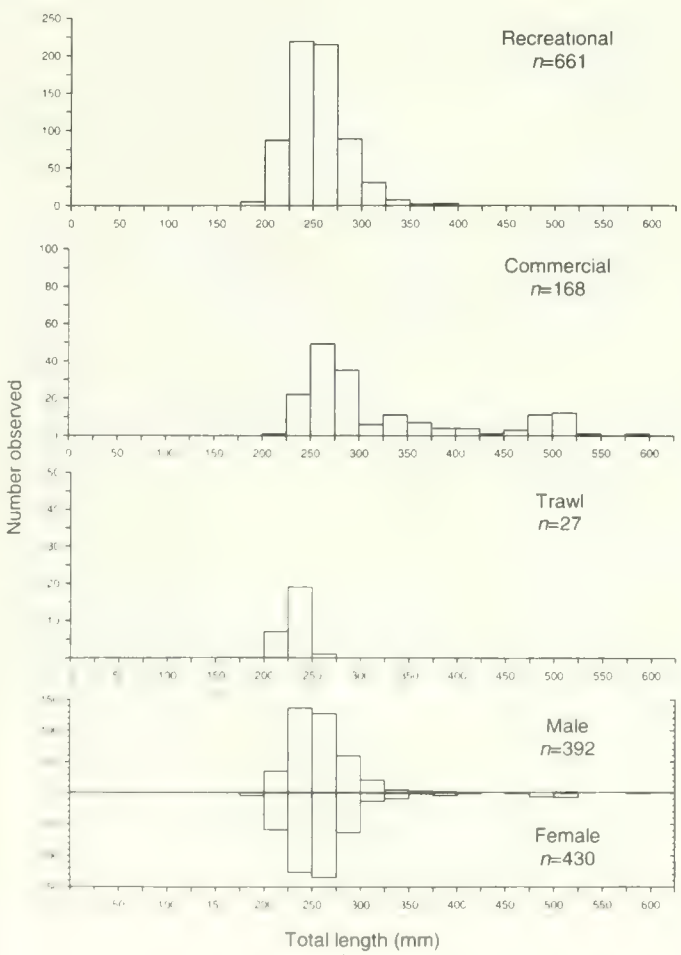

Figure 2

Total lengths of vermilion snapper from the eastern Gulf of Mexico by sampling source and by sex.

cantly different from 1:1 (χ^2=1.175, df=1, P>0.05). Seasonal sex ratios based on three-month intervals (December–February, March–May, June–August, September–November) ranged from 1:1 to 1:1.2 and were not significantly different from 1:1 (χ^2 =0.017 to 1.045, df=1, P>0.05).

Age and growth

Under reflected light, alternating opaque (white) and translucent (dark) zones were evident on vermilion snapper otoliths (Fig. 1). Two readers examined a subsample of 200 otoliths, and 57% of their readings were in agreement. Most of the disagreements (82.6%) differed by only one opaque zone. A second independent reading of the subsample by the two readers resulted in complete agreement (100%). Of 858 sectioned otoliths examined, 841 (98%) could be assigned ages. Of the otoliths that could be aged, measurements for marginal-increment analyses could not be made for 50 individuals (5.9%) because of broken or occluded areas along the otolith radius.

Analyses of marginal-increment data for fish ages 2 to 10 suggested that opaque zones were formed once a year during the late spring to early summer (Fig. 3). During this time, the widest increments (opaque zone formation was imminent) and the narrowest increments (opaque zone formation was just completed) were present. In addition, monthly median marginal increments for ages 2 to 10 had a consistent yearly pattern of high me-

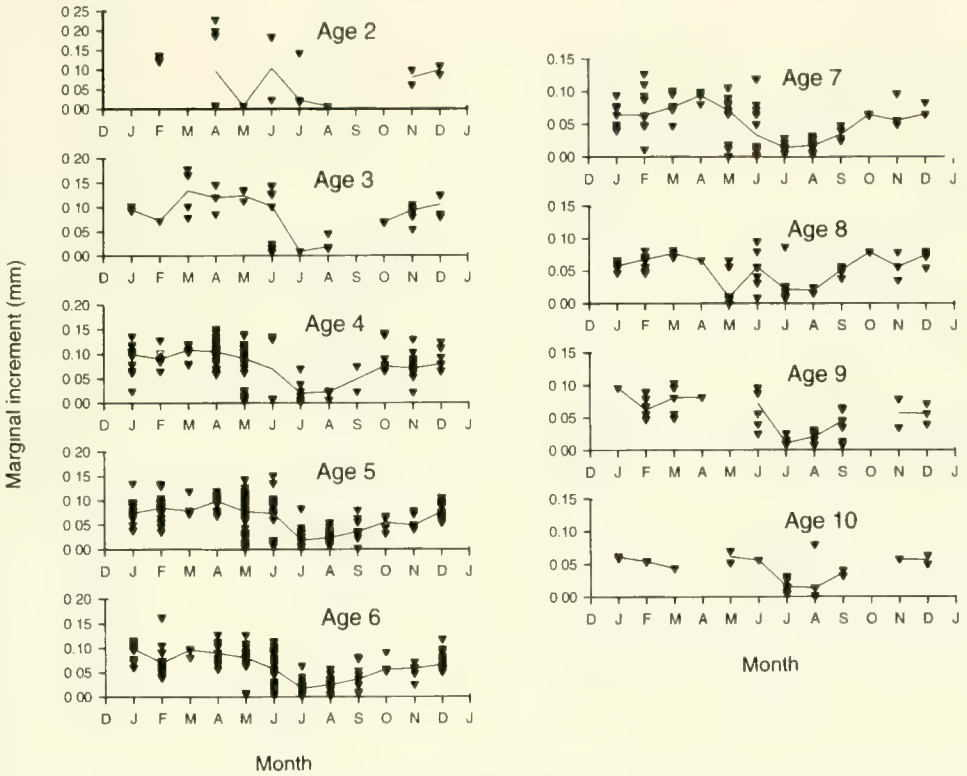

Figure 3

Marginal increments from sectioned otoliths of vermilion snapper ages 2–10 years from the eastern Gulf of Mexico. Median monthly increments are identified by the solid line.

dian values from January to May and low values in July and August (Fig. 3).

Ages ranged from 1 to 13 years. Most males (74%) and females (77%) were found to be between ages 4 and 7 (Fig. 4). Initial growth of vermilion snapper was rapid, and fish attained a mean length of 211 mm TL during their second year (age 1, Table 3). However, subsequent increases in length were low (<33 mm). Likelihood ratio tests did not show a difference between the male and female von Bertalanffy growth models (χ^2=0.92, df=3, P>0.5). The estimated von Bertalanffy growth parameters (standard error) for all aged fish (n=841) were L_∞=298(5.0), K=0.25 (0.04), and t_0=–3.9 (0.85). Predicted lengths at age were similar to mean lengths at age (Table 3; Fig. 5); however, because of high variability in length-at-age data, the correlation coefficient for estimated growth was low (adjusted r^2=0.26), suggesting that age is not a good predictor of length.

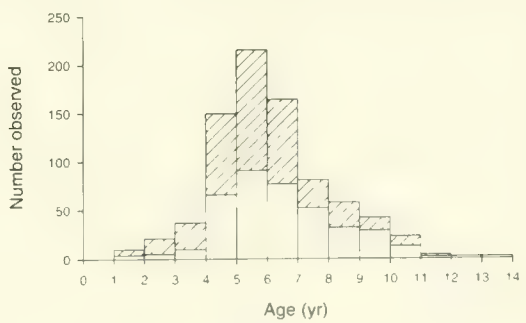

Figure 4

Age distribution of male (open) and female (hatched) vermilion snapper from the eastern Gulf of Mexico.

Mortality

Catch length-frequency data were transformed into age frequencies by using age-length keys constructed from our ages. Full recruitment into both the recreational and commercial fisheries occurred at age 6. Survivorship (standard error) estimates determined by using the Chapman-Robson method were 0.619 (0.0002) and 0.613(0.0001), respectively. Instantaneous mortality estimates (Z=–ln survivorship) were

Table 3

Mean empirical and predicted total lengths (mm TL) of female, male, and all vermilion snapper sampled from the eastern Gulf of Mexico. Standard error is in parentheses, and n is number of fish examined.

	Female			Male			All Fish			
Age	n	Mean empirical	Range	n	Mean empirical	Range	n	Mean empirical	Range	Predicted
1	6	214(13.1)	195–225	4	207(4.6)	202–212	11	211(10.1)	195–225	210
2	16	224(16.3)	200–255	5	221(13.4)	208–243	21	223(15.4)	200–255	229
3	27	249(24.7)	200–302	10	253(36.1)	225–347	37	250(27.8)	200–347	245
4	83	253(41.9)	202–518	66	245(23.8)	199–322	154	253(41.5)	199–518	257
5	124	267(60.5)	192–518	91	262(41.5)	215–505	225	270(60.8)	192–518	266
6	88	275(60.1)	205–515	76	262(29.7)	218–385	171	274(56.9)	205–515	273
7	29	263(23.7)	223–340	52	259(21.0)	225–315	85	267(43.1)	223–502	278
8	26	294(67.7)	235–500	32	270(14.8)	241–300	59	282(48.1)	235–500	283
9	13	277(21.8)	250–333	29	288(63.6)	325–585	45	293(64.4)	235–585	286
10	10	294(38.1)	267–397	13	295(69.6)	240–515	24	294(55.7)	240–515	289
11	2	281(8.5)	275–287	2	313(40.3)	284–341	4	297(29.9)	275–341	291
12				2	271(0)		2	271(0)		292
13				2	284(32.5)	261–307	3	304(42.1)	261–345	294

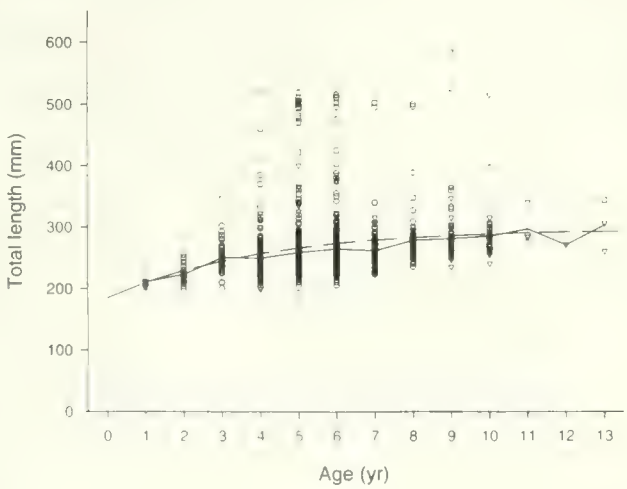

Figure 5

Total length at age, mean length at age (solid line), and predicted length at age (dashed line) for vermilion snapper from the eastern Gulf of Mexico. Circles = females, triangles = males, and squares = unknown sex.

0.480 for the recreational fishery and 0.489 for the commercial fishery.

Reproduction

Our sample contained no immature males and only 23 immature female vermilion snapper. Testes either contained tailed sperm, suggesting the potential for spawning, or contained brown bodies, suggesting previous spawning. The smallest male examined was 199 mm TL; therefore males must reach maturity at a smaller size than do females. For females, 80% were sexually mature at age 1, and 100% were sexually mature by age 7. More than 90% of the females were mature at 200 mm TL, and 100% were mature at 325 mm TL.

Vermilion snappers in the eastern GOM spawn from May to September. Ripe females were observed during this time period (with the exception of June) (Fig. 6). These fish contained late-stage vitellogenic oocytes, hydrated oocytes, and postovulatory follicles (Fig. 7). Through the rest of the year, there was a progression from mostly resting ovaries during October to mostly early developing ovaries during December. Ripe males were observed throughout the year; they were most common (>60% of testes) from March to September and in January (Fig. 6). For both sexes, median GSIs were low from October to April (<0.01 for females and <0.005 for males, Fig. 8). In May, GSIs increased dramatically (medians equaled 0.034 for females and 0.020 for males) and then gradually decreased through September.

Vermilion snapper batch fecundities ranged from 5535 to 86,811 oocytes from fish measuring 210–298 mm TL (n=27). The relationship between batch fecundity and length was batch fecundity = 317 × (whole weight) – 3.1624×10^4, r^2=0.55.

Discussion

Collections

The vermilion snapper that we sampled from the eastern GOM were smaller than those collected during the 1980s from the western GOM. Most hook-and-line-caught fish that we sampled (88%) were between 201 and 325 mm TL and were smaller than fish collected from the Texas Flower Gardens by Zastrow (1984) and Nelson (1988). The fish they sampled were mostly (75%) between 269 and 474 mm TL and 262 and 517 mm TL, respectively. Gear bias is probably not responsible for the differences in length distributions. As in our study, both Zastrow (1984) and Nelson (1988) examined fish caught principally with hook-and-line gear. Furthermore, Nelson (1988) examined the length distributions of vermilion snapper caught with different hook sizes (Mustad no. 2–no. 4/0) and noted no differences in the size of fish caught.

Other factors, such as depth and movement, probably cannot explain the differences between the size distribution of fish caught in our study and that of fish caught in the western GOM. Nelson (1988) caught most vermilion snapper from depths between 60 and 90 m. We do not know the depth at which the fish we sampled were captured; however, the mean depth at which vermilion snapper were caught by the eastern GOM commercial fishery in 1995 was 80 m (Schirripa[4]) and is within the depth range given by Nelson (1988). The presence of larger fish in the western GOM could be the result of larger fish moving from the eastern to western GOM. However, this movement seems unlikely because tagging data suggest that vermilion snapper are residents of reefs and do not travel long distances (Beaumariage, 1964; Fable, 1980; Grimes et al., 1982).

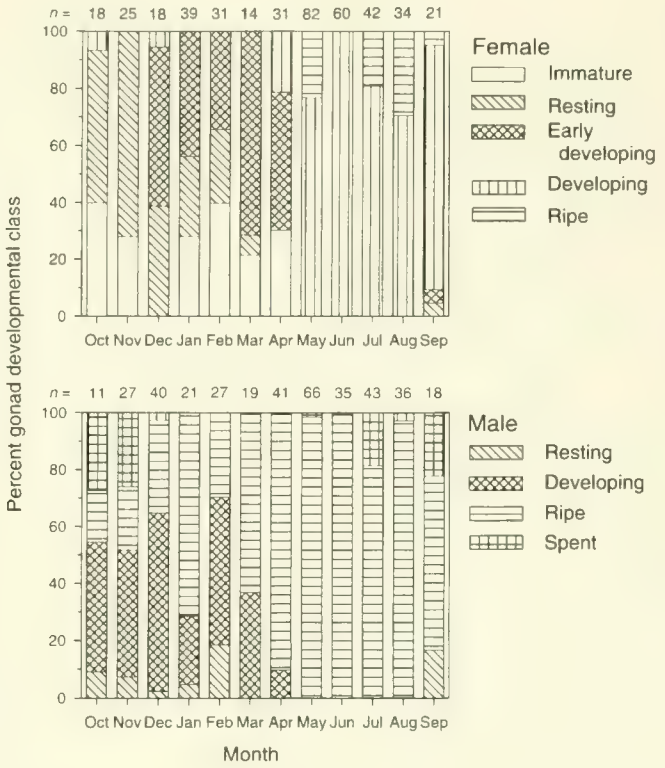

Figure 6

Percentage of vermilion snapper from the eastern Gulf of Mexico in gonad development classes by month and by sex.

Increases in fishing pressure may have reduced the average size of fish caught by the fishery. Schirripa[4] reported that the average size of fish in the GOM commercial fishery dropped from a high of 371 mm TL in 1984 to a low of 320 mm TL in 1993. Over this same time, commercial landings increased from 1.6 million pounds in 1984 to 2.5 million pounds in 1993, and recreational landings increased from 0.2 million fish in 1984 to 1.2 million fish in 1993.

The sex ratio of GOM vermilion snapper is different from the sex ratio reported for snapper from the SAB. In the GOM, female-to-male sex ratios were not significantly different from 1:1 (Zastrow, 1984; Collins[3]; this study), or they significantly favored males (1:1.2; Nelson, 1988). In the SAB, females significantly outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Cuellar et al., 1997; Zhao and McGovern, 1997). Zhao and McGovern (1997) partitioned sex ratios from the SAB by depth, fish size, sampling year, gear type, and latitude. Of these, only gear type and latitude significantly affected the sex ratio. Females were proportionally more common in trap and hook-and-line collections than in trawl collections. Although Zhao and McGovern (1997) were cautious about attributing decreases in the proportion of females to changes in latitude, 1:1 sex ratios reported in the GOM (Zastrow, 1984; Collins[3]; our study) and from Puerto Rico (Boardman and Weiler, 1979) are consistent with this hypothesis. We did not find any significant differences in sex ratios by season; however, Zastrow (1984) and Nelson (1988) reported an increase in the proportion of males in the summer in the western GOM.

Age and growth

Sectioned otoliths can be used to age eastern GOM vermilion snapper and produce higher readability

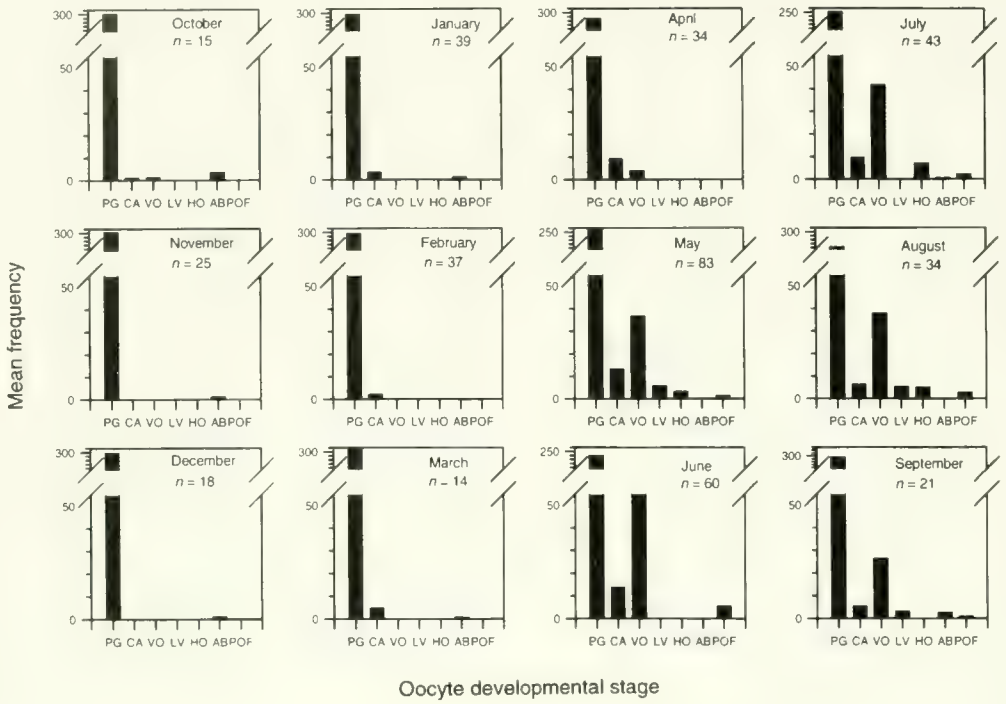

Figure 7

Average frequency of occurrence of oocyte development stages by month for vermilion snapper from the eastern Gulf of Mexico. PG=primary growth oocyte, CA=cortical alveolar oocyte, VO=vitellogenic oocyte, LV=late vitellogenic oocyte, HO=hydrated oocyte, AB=atretic body, and POF=postovulatory follicle.

and agreement rates than scales or whole otoliths can produce. Our readability rates were high (98%) and were similar to rates reported by Zhao et al. (1997), who were able to read 96% of sectioned otoliths from SAB vermilion snapper. The use of whole otoliths has produced mixed results. Barber (1989) had a high agreement rate between readings (84%) and was able to count as many as 26 zones. However, Grimes (1978) found that whole otoliths were difficult to interpret at ages greater than 7. Scales have been used with limited success by Grimes (1978), Zastrow (1984), Nelson (1988), and Collins and Pinckney (1988). Agreement rates between readings in these studies have ranged from 44% to 85% and were lower than reported in this study (100%) and by Zhao et al. (1997) (96%). Grimes (1978) found that counts from scales and whole otoliths from the same fish were similar and reported an agreement rate of 75%.

Marginal-increment analyses suggest that vermilion snapper form one opaque band per year in the late spring and summer. This pattern has also been noted for vermilion snapper captured from the SAB. Zhao et al. (1997) found that opaque zones formed in June for fish age one year and in July for fish ages two to six years. Barber (1989) attempted to use marginal-increment analyses to validate annulus formation in whole otoliths from snapper from the GOM; however, he was unable to show an annual pattern. Grimes (1978) observed that the hyaline layer was formed in November in the SAB. Because hyaline and opaque bands alternate, Grimes's (1978) findings imply that an opaque band is formed once a year before November.

Vermilion snapper are considered long-lived, slow-growing fish (Manooch, 1987). The oldest individual we aged was 13 years old, similar to the SAB maximum age of 12 years reported by Zhao et al. (1997), who also used sectioned otoliths. However, our maximum age was older than the scale-based maximum ages reported for the western GOM of age 7 by Zastrow (1984) and age 10 by Nelson (1988). Those using scales to age fish typically underestimate the ages of older fish (Beamish and McFarlane, 1987). As fish approach their asymptotic size, little or no increase in fish size occurs and this is reflected as little or no increase in scale size. Therefore, rings at the scale edge of older (larger) fish become difficult

to interpret. Barber (1989) reported that otolith-based ages were on average three years greater than scale-based ages for GOM vermilion snapper, although he did not directly compare otoliths and scales from the same fish. Our maximum age was less than the 26 years reported by Barber (1989). His older ages are surprising because he used whole otoliths to estimate age. Grimes (1978) noted that one disadvantage to aging vermilion snapper by using whole otoliths is that rings are difficult to interpret in fish older than age 7. Although we did not compare whole otoliths to sectioned otoliths of vermilion snapper, for gag (*Mycteroperca microlepis*), annuli at the edge of the otolith are more readily observed in sectioned otoliths than in whole otoliths (Collins et al., 1987; Hood and Schlieder, 1992).

Empirical mean lengths and predicted lengths at age were less for our vermilion snapper than for snapper from the western GOM (Table 4; Fig. 9). At age 1, the mean length of fish from our study (211 mm TL) is similar to that of fish from studies by Zastrow (1984; 207 mm TL) and Nelson (1988; 207 mm TL); however, by age 4, the mean length in our study (253 mm TL) is at least 100 mm less than mean lengths in their studies (353 and 357 mm TL , respectively; Fig. 9). If scale-based ages underestimate actual age, then mean length at age and growth rates will be overestimated (Beamish and McFarlane, 1987). However, because scales generally give good estimates of age for younger fish and because the mean length of our fish at age 1 is similar to lengths given by Zastrow (1984) and Nelson (1988), differences in length could reflect differences in growth as opposed to bias from aging structures.

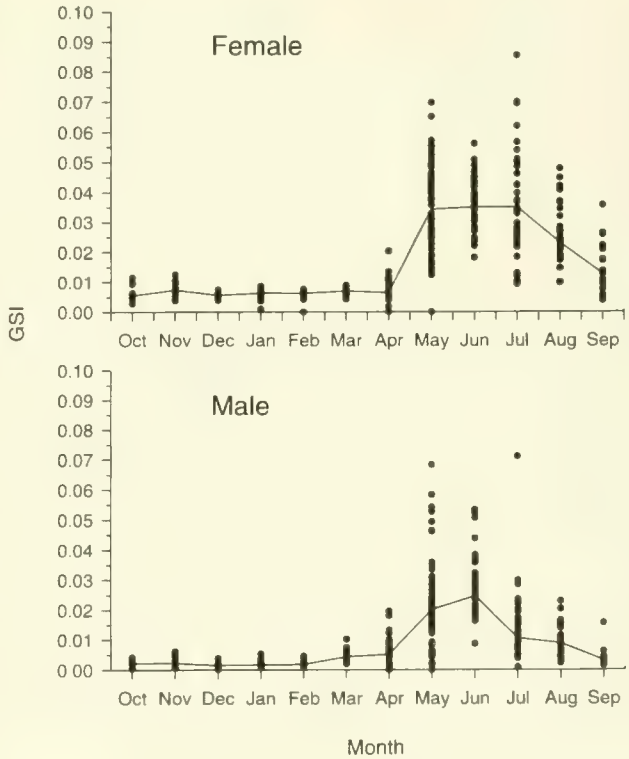

Figure 8

Monthly gonosomatic indices (GSI) for female and male vermilion snapper from the eastern Gulf of Mexico. Median values are connected by the solid line.

Our estimates of empirical mean lengths and predicted lengths at age, which were lower than those estimates for vermilion snapper from the western GOM, could also be the product of changes in fishing pressure. Schirripa[4] summarized GOM landings data and noted that annual commercial and recreational landings have increased 3- to 4-fold from the mid-1970s to the early 1990s. If larger fish are more vulnerable to capture, then faster-growing fish within an age class will be selectively removed from the population. The result of this type of selection will be a depression of mean size at age for older age classes and an underestimation of the biologically realistic L_∞ (Pitcher and Hart, 1982). This pattern was noted by Zhao et al. (1997) for vermilion snapper in the SAB. Their estimates of growth based on ages from sectioned otoliths for 1979–81 were similar to growth estimates (scale-based ages) by Grimes (1978) from the mid-1970s, when fishing pressure was low. Zhao et al.'s (1997) estimates of size at age and of L_∞ then decreased over time. Estimates of L_∞ dropped from 629 mm TL (1979–81) to 365 (1982–84) and 333 mm TL (1985–93) (Table 4). They could not attribute declines in size at age or L_∞ to gear selectivity, sampling regime, depth, or latitude and concluded their observed changes were due to selective fishing for faster-growing individuals within all age classes.

Similar decreases in observed lengths at age have been reported for red porgy, a species often found in the same habitats as vermilion snapper (Grimes et al., 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984; Nelson, 1988) and sought by the same fisheries (Grimes et al, 1982; Nelson, 1988; Collins and Sedberry, 1991). Average total length of GOM red porgy reported by Hood and Johnson[7] at age 6 years was 348 mm and was over

[7] Hood, P. B., and A. K. Johnson. 1997. Age, growth, mortality, and reproduction of red porgy (*Pagrus pagrus*) from the eastern Gulf of Mexico. Florida Marine Research Institute, Florida Department of Environmental Protection, 100 Eighth Avenue S.E., St. Petersburg, Florida. Manuscript in prep.

100 mm less than the average length of 464 mm reported by Nelson (1988). In the SAB, the average total length of 6-year-old fish had decreased from 451 mm in 1972–74 (Manooch and Huntsman, 1977) to 363 mm in 1991–94 (Harris and McGovern, 1997). Both Harris and McGovern (1997) and Hood and Johnson[7] concluded that the observed decrease in average length at age was likely due to size selective fishing.

Mortality

The age of full recruitment to both the recreational and commercial fisheries has increased since the early 1980s. Zastrow (1984) and Nelson (1988) reported the age at full recruitment to be 4 years, less than our estimate of 6 years. The reported age of full recruitment to the SAB hook-and-line fishery was 4 years before 1981 (Grimes, 1978; Huntsman et al., 1983; Zhao et al., 1997) but increased to 6 years by 1993 (Cuellar et al., 1996; Zhao et al., 1997). This increase in age of recruitment has been associated with a decrease in length at age attributed to selective fishing on faster-growing members of each age group (Zhao et al., 1997). Our estimates of mortality (0.469–0.489) are within the range given by Schirripa[4] for the years 1986–1995 in the GOM (0.466–0.791) and less than the estimate from the SAB headboat fishery (0.67) reported by Huntsman et al. (1983).

Reproduction

Our observed sizes of maturation were less than those reported by Nelson (1988) for the western GOM. We found that most females were sexually mature at 200 mm TL (age 1), and we did not examine any immature males (the smallest male we sampled was 199 mm TL). The smallest mature female and male reported by Nelson (1988) were 234 mm TL and 291 mm TL, respectively. In the SAB, Collins and Pinckney (1988) found that at 160 mm TL, 60% of females and 90% of males were mature. Cuellar et al. (1996) sampled females as small as 186 mm TL and males as small as 197 mm TL and did not find any immature fish in their samples. These lengths at maturity are in contrast to the results of Grimes and Huntsman (1980) who found that SAB vermilion snapper matured between 186 and 324 mm TL (ages 3 and 4). There is an indication that increasing fishing pressure may depress vermilion snapper size and age at maturity. Zhao and McGovern (1997) noted a decrease in the size at maturity for males and females in the SAB from 1970 to 1992. Before 1982, 31% of males and 5% of females were mature at 140 mm TL. After 1982, all males and 37% of females were mature at 140 mm TL. They suggested that this change may have been caused by the increasing and selective fishing pressure that occurred during the 1980s.

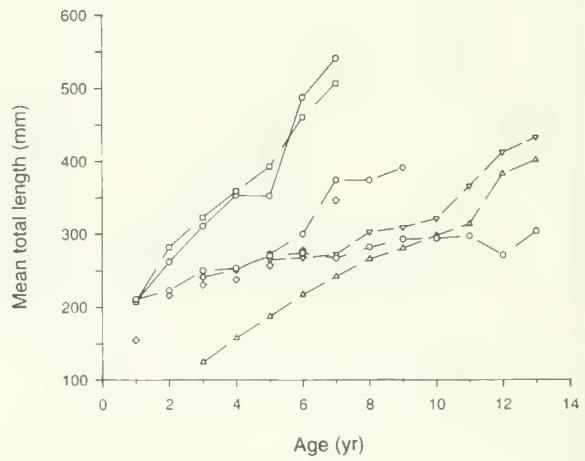

Figure 9

Mean empirical total length at age for vermilion snapper from the eastern and western Gulf of Mexico. Scale-based ages from the western Gulf of Mexico by Zastrow (1984; circle, solid line) and Nelson (1988; square). Scale-based ages from Barber (1989) from the eastern (diamond) and western (hexagon) Gulf of Mexico. Whole-otolith-based ages from Barber (1989) from the eastern (triangle) and western (inverted triangle) Gulf of Mexico. Sectioned-otolith-based ages from this study (circle, dashed line).

On the basis of the presence of ripe females and increases in GSI, we believe that vermilion snapper in the GOM spawn from May to September. Nelson (1988) and Collins[5] also reported summer spawning. In our samples, ripe gonads were present from late spring to early fall but were most common from May to July. In addition, GSIs were highest during the summer months. Spawning seasonality in the GOM is similar to that reported for the SAB, where fish spawn from the late spring to early fall (Grimes and Huntsman, 1980; Cuellar et al., 1996). Boardman and Weiler (1979) found that in Puerto Rican waters, spawning takes place year round.

Batch fecundity was positively correlated with fish length. Nelson (1988) and Collins[5] also found a positive relationship between batch fecundity and length for GOM fish. Their estimates were larger than those obtained in our study (61,600–392,000 and 33,550–415,161 oocytes, respectively); however, the fish sampled were also larger (209–510 and 248–375 mm TL, respectively). Our estimates of batch fecundity were similar to SAB estimates reported by Cuellar

Table 4

Von Bertalanffy growth parameters for vermilion snapper from the Gulf of Mexico (GOM) and South Atlantic Bight (SAB). Table adapted from Goodyear and Schirripa.[3] Our study and the studies of Schirripa[4] and Zhao et al. (1997) were added to the table. L_∞ is the asymptotic TL, K is the von Bertalanffy growth coefficient, t_0 is the time that TL is zero, and n is the sample size.

Study and area	Aging structure	Sex	n	L_∞ (mm)	K	t_0
Current study						
Eastern GOM	otoliths	Combined	841	298	0.25	–3.9
Schirripa[1]						
GOM	scales and otoliths	Combined	586	535	.203	–0.94
Nelson (1988)						
Flower Gardens, TX	scales	Combined	906	554	0.22	–0.30
Barber (1989)						
St. Petersburg, FL	scales	Combined	34	936	0.05	–3.37
Pensacola, FL		Combined	194	344	0.16	–3.356
Galveston, TX		Combined	799	561	0.10	–2.81
Port Aransas, TX		Combined	270	428	0.15	–2.78
Brownsville, TX		Combined	779	477	0.16	–2.32
St. Petersburg, FL	otoliths	Combined	1113	469	0.09	–1.16
Pensacola, FL		Combined	600	511	0.08	–1.44
Galveston, TX		Combined	799	554	0.08	–1.46
Port Aransas, TX		Combined	270	657	0.07	–1.18
Brownsville, TX		Combined	779	603	0.09	–0.87
Grimes (1978)						
SAB	scales	Combined	815	627	0.20	–0.13
Zhao et al. (1997)						
1979–81	otoliths	Combined	195	629	0.202	–0.117
SAB 1982–84		Combined	265	365	0.315	–0.361
1985–93		Combined	766	333	0.271	–0.899

[1] Schirripa, M. J. 1992. Analysis of age and growth of vermilion snapper with an assessment of the fishery in the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Miami, FL. CRD-91/92-

et al. (1996; 4000 to 90,000 oocytes from fish 186–340 mm TL).

Summary

Recent stock assessments of vermilion snapper suggest that vermilion snapper stocks in the GOM are overfished (Schirripa[4]). Our study, when compared to previous studies of vermilion snapper, suggests that size-selective mortality coupled with overfishing may be responsible for changes in life history parameters (decreases in the mean length at age, estimated L_∞, and length and age of maturation). If these changes are not taken into consideration, estimates of the yield-per-recruit, mortality, and spawning potential ratios that use the above life history parameters in their calculations could be biased. Consequently, erroneous conclusions about the health of the stock of GOM vermilion snapper could be made in future stock assessments.

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Movement of Atlantic cod, *Gadus morhua*, tagged in the Gulf of Maine area

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Abstract.—Over 22,000 Atlantic cod, *Gadus morhua*, were tagged with T-bar tags and released in the Gulf of Maine area in 1984–97 and 2400 recovered tags were used to interpret movement of tagged fish. Most of the releases were of adult fish made during the winter cod spawning season from aggregations found on known spawning banks. Recaptures by NAFO divisions were weighted with an annual index of fishing effort to account for probability of recapture. At the division level, very little exchange between the area east of 4X and the Gulf of Maine was evident. However, within the Gulf of Maine an exchange of about 15% between 4X and 5Z and somewhat higher between 4X and 5Y was apparent. Cod tagged on Browns Bank and Georges Bank during the spawning season showed widespread dispersal both within their respective division and to adjacent divisions. The seasonal distribution of recaptures in 4X indicates aggregation for spawning followed by postspawning dispersal. The seasonal pattern for Georges Bank is less clear but there are indications of net loss to the 4X area. Distribution of recaptures from Georges Bank releases in 1994 was similar to those observed for releases made in 1984–85. Results of the study were consistent with results from earlier tagging experiments and demonstrate substantial interaction of cod from different management areas. These findings may have implications for stock assessment models and management objectives.

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The Atlantic cod (*Gadus morhua*) is a demersal species with a wide Northwest Atlantic geographic range extending from the Gulf of Maine in the south to the Davis Strait in the north (Scott and Scott, 1988). It is one of the most important commercially exploited groundfish species in Atlantic waters off Canada and the eastern U.S. region, and cod stocks have supported fisheries in the Gulf of Maine since the 1700s (Serchuk and Wigley, 1992).

The Gulf of Maine area, as defined in this study, includes waters of the Bay of Fundy, Georges Bank to 71°41'W, and the Scotian Shelf west of 63°20'W, an area of approximately 150,000 km^2. There are four fisheries management units identified for Atlantic cod in this area, based on known areas of spawning aggregation and commercial fisheries (Halliday et al., 1986). Geographic boundaries of North Atlantic Fisheries Organisation (NAFO) divisions and the U.S. National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) unit areas (Fig. 1) are used to approximate the distribution of the stocks. The present management units are division 4X, subdivision 5Ze in unit areas j and m (Canada), subdivision 5Zw+SA6 (USA) and division 5Y. The area is also divided by the International Maritime Boundary (IMB) between Canada and the United States, established in 1984. Halliday and Pinhorn (1990) have provided an extensive review of the basis for existing statistical areas used to report fisheries activities and note that unit areas were established in the early 1970s.

Population characteristics of the four cod stocks have been reported by Canada (Clark 1996; Hunt and Buzeta 1996) and by the United States (NEFSC, 1994). Stock abundance has shown substantial variation in the last fifteen years and a broad range of recruitment. In general, all the stocks have declined from the long-term average abundance and, with the exception of the 4X stock, appear to be at low levels of spawning stock biomass.

Numerous tagging studies have been undertaken to examine movement of cod in the Gulf of Maine area. Hunt and Neilson (1993) provided a synopsis of tag-recapture

results from experiments conducted between 1923 and 1960. An earlier summary of cod tagging studies is given in Wise (1963). Templeman (1962) provided a comprehensive summary of the basis for separating cod stocks in the northwest Atlantic using meristic and results of tagging experiments and concluded "there are Browns Bank and eastern Georges Bank stocks, probably essentially separate as spawning stocks but with some intermigration in both directions across the Fundian Channel and some intermingling of both these stocks with those of southwestern Nova Scotia." In general, results of these early experiments indicate substantial movement of cod within the 4X area and to a lesser extent to and from the adjacent 5Y and 5Ze areas. The pattern of recapture locations shows a general dispersal from the area of release and some increase in the number of cod moving with elapsed time. However, it is difficult to interpret these studies as proportional movements because landings and effort are generally not available for weighting probability of recapture by area.

Canada has conducted a number of tagging studies on cod in the Browns Bank, Georges Bank, and Bay of Fundy areas since the 1970s. Studies conducted between 1994 and 1996 were part of a co-operative research study involving Canada and the United States. This report provides an interpretation of cod movements in the Gulf of Maine area based on results of recaptures of cod tagged in the 1979–97 time period.

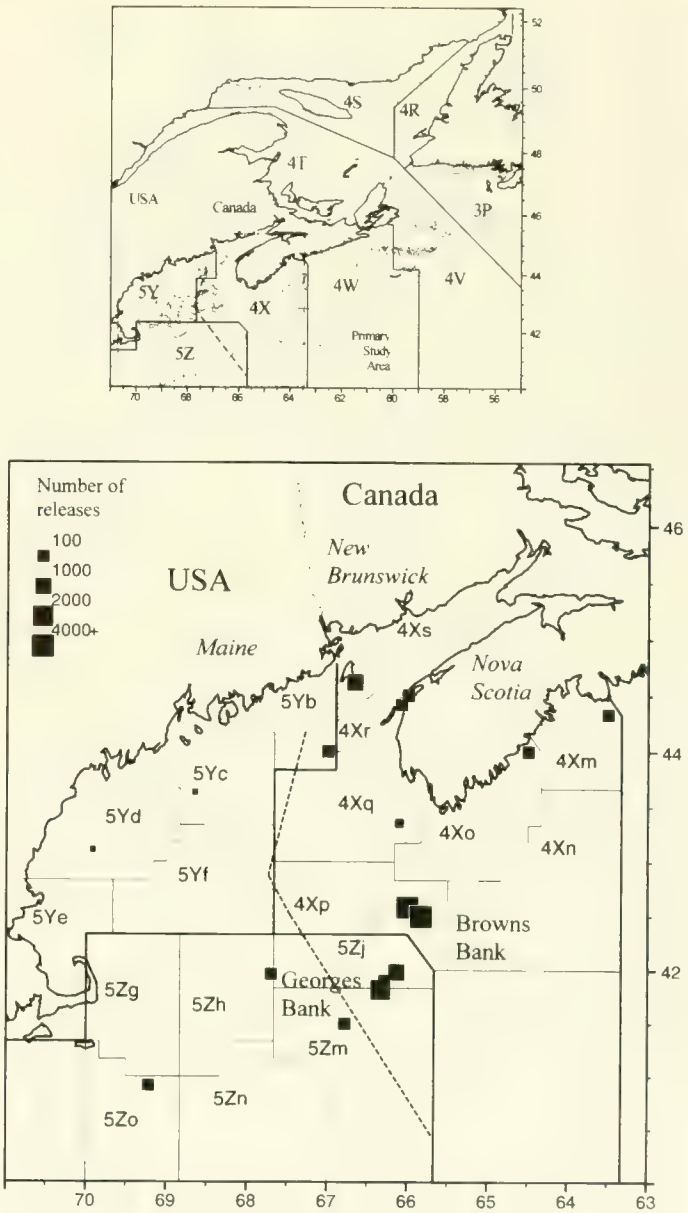

Figure 1

North Atlantic Fisheries Organization (NAFO) division (4X, 5Y, 5Z) and unit areas (eg. 5Zj) boundaries in the Gulf of Maine area and cod tag release locations. The dashed lines indicates the International Maritime Boundary line between Canada and the United States.

Methods

Canada has conducted stratified random bottom trawl surveys in the Gulf of Maine since 1970 and on Georges Bank since 1986. The United States has also conducted similar surveys in the spring (1968) and fall (1963) of each year. Indices of abundance derived from these surveys are routinely used in stock assessment models to estimate population abundance (Hunt and Buzeta, 1996), and they provide a synoptic view of cod distributions in the Gulf of Maine area during both spawning and postspawning seasons. The mean catch per tow, aggregated by ten-min latitude and longitude squares, was calculated for the U.S. spring and fall research-vessel time series. These surveys cover most of the Gulf of Maine area, compared with the Canadian summer survey (4X only) and Canadian winter survey (5Ze only), and therefore provide a distribution pattern for cod in the entire study area.

Tagging locations were determined from areas of high catch rates in research vessel surveys, as well as the location and timing of historical cod spawning activity. Additional tagging was completed during other times in areas of fishing activity or special interest locations. Fishing trials were used to identify sites with high catch rates and at least 50% cod composition, and new sites were selected when catch rates or cod composition declined. Typically, once an aggregation of cod was located, fishing and tagging continued at that site for 1–2 days. Areas with high

catches of skates (*Raja* spp.) and dogfish (*Squalus acanthias*) were avoided because their abrasive skin resulted in damage to cod and poor quality specimens for tagging.

Fisheries research stern trawlers, 50–70 m in length, equipped with a research Western IIa otter trawl and with wet laboratory facilities below the trawl deck, were used for large-scale tagging operations. Fishing operations consisted of 5–20 min tows at depths ranging from 40 to 70 fathoms. At the end of each tow, cod were released into a sluice way leading to the below-deck wet laboratory area and transferred into 1500-L holding tanks with recirculating ambient sea water. Viability of each cod was assessed prior to tagging and fish in poor condition or that had apparent external injuries were discarded. Control experiments to assess tag or stress induced mortality were not conducted, but observation showed that even fish that were initially inverted or dormant on the bottom of the tank returned to an apparent active and normal behavior within 15–30 minutes. Tagged fish were released through a sluice way exiting about one to two meters above the water line. Approximately 100 to 250 cod could be held, tagged, and released from each tow, depending on average fish size in a tow.

Fish to be tagged were removed from holding tanks by hand with dip nets and placed on a measuring board to obtain length. A tag was inserted near the leading edge of the first dorsal fin and the fish was released. Total elapsed time from start to end of the tagging operation was in most cases less than 30 seconds for each fish. An *ad hoc* representative sample was examined to verify the spawning state of reproductive development (Hunt, 1996) but results were not recorded.

Several small-scale cooperative studies were carried out with commercial fishing vessels. The first of these opportunistic tagging operations was conducted aboard the U.S. FV *Mary V*, a longline vessel fishing out of Gloucester, MA. During routine fishing operations on the northern edge of Georges Bank, cod caught that were less than the U.S. minimum legal size (49 cm 19 inches) were tagged by the vessel's crew and released. Tags were also supplied to staff of the Massachusetts Division of Marine Fisheries (MA-DMF) and the Maine Department of Marine Resources (ME-DMR) to use during trips when onboard fishery observers were present on commercial longliners fishing in the Nantucket Shoals (MA-DMF) and on commercial charter boats fishing the inshore waters of the Gulf of Maine (ME-DMR). During these trips, undersize cod were also tagged and released. A small number of cod, taken as bycatch in lobster traps during the winter lobster fishing season (4Xq inshore), were tagged and released by Canadian fishermen.

All tags were of the T-bar type (FD-67 and FD-94 in 1994) applied with the Mark-II tag insertion gun and were supplied by Floy Tag and Manufacturing, Inc (4616 Union Bay Place NE, Seattle, WA 98105). Overall length of the tag was about 6.5 cm and each tag had a 3.5-cm bright yellow address sleeve and a 1.0-cm attachment T-bar. Each tag was imprinted with a unique identification number and Canadian return mail address on the vinyl sleeve. Tags used in the 1994 experiment included a second mailing address for the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center, Woods Hole, MA. Tags were provided in clips of fifty with consecutive numbering to facilitate record keeping.

An extensive advertising campaign, targeting Canadian and U.S. fishing enterprises and communities, was completed prior to and after each of the large-scale tagging experiments. This included notices in local newspapers and other industry publications, all-weather bilingual posters located at major fish landing and processing facilities, personal contact with industry representatives, and follow-up with individuals submitting tags. A representative of the fishing sector participated in the 1994 experiment to obtain firsthand knowledge of operations and, as was hoped, to convey the importance of returning tags to colleagues.

In Canada, a nominal reward of seven dollars was offered for each tag returned. In the United States, a reward of five dollars was paid for tags returned with recapture information and two dollars for tag only returns. In addition to the reward, the finder was provided with a summary of release and recapture information for each tag returned.

All release and recapture data were loaded to a database to facilitate analysis. Tag-recapture information was edited to eliminate obvious errors such as onshore recoveries, substantial decreases in fish length, unrealistic travel and elapsed time factors, etc. Quality of recapture data was variable, ranging from no information to a detailed record of how, when, and where (latitude and longitude) fish were caught, fish size at recapture, age determination material, and other anecdotal information. About 80% of recaptures included detailed information on location and about 20% had length-at-recapture measurements.

Analysis of recapture data was completed first at the divisional level, then at the unit area level for the Gulf of Maine and finally at 10-min latitude and longitude squares. Results were compiled to show movement from area of release to adjacent areas and, conversely, movement to an area from adjacent sites. Analysis of recapture patterns at the divisional level

was used to assess exchange between management areas. Observed numbers of returns were used for this purpose because exploitation rates and commercial fishery landings, required for weighting, were not as readily available for areas outside of the Gulf of Maine area. All releases and recaptures in divisions 4W, 4V, 4T, 4R, 4S, and subarea 3, which were geographically east of the division 4X-4W boundary, were grouped for this part of the analysis; we refer to this combined geographic area as "east of 4X."

Because recaptures from tagging studies are usually dependent on commercial fisheries, the distribution and abundance of recaptures is a function of the distribution of fishing effort as well as of fish movements. In an attempt to account for the effect of fishing effort, we weighted recaptures using the commercial fishery exploitation rates for cod stocks in the area. Landings, effort, and exploitation rates of cod by unit area were obtained from the published literature (NEFSC, 1994; Clark, 1996; Hunt and Buzeta, 1996). No provision was made for potential discarding, misreporting of catches, or allocation to unit area. The extent of these problems in landing statistics are thought to be substantial in some years and areas but have not been quantified (Clark, 1996; Hunt and Buzeta, 1996). A review of both the quality and quantity of effort data indicated that a low proportion of landings, particularly for fixed gear components, were represented. Therefore, direct measures of effort could not be used to make adjustments to returns on the basis of distribution of effort. However, trends in landings by unit area and fleet composition showed a relatively stable spatial and seasonal pattern. In some years a considerable proportion of total Canadian landings from division 4X was not allocated to a specific unit area. On the basis of preliminary work by Clark (1996), an algorithm was applied to allocate this unspecified proportion to unit area. The reported annual exploitation rate for each stock was then partitioned according to annual percent of unit area landings and used as a year- and area-specific index of the probability of recapture:

$$A_{a,y} = \Sigma C_y / (C_{a,y} \times E_y),$$

where A = adjustment factor;
C = percent of annual reported landings by management area;
E = reported annual exploitation rate by management area;
$_a$ = unit area; and
$_y$ = year.

Within a year, tag recaptures from areas with low landings were therefore given higher relative weighting than those from areas of high landings. Annual differences in exploitation rate were used to weight for between-year effects. The derived adjustment factors were standardized to the unit area and year with the lowest landings and exploitation rate.

Summaries of tag recaptures within an area by area of release required standardisation to reduce the impact of large numbers of releases from some areas. For example, the large number of releases from the Browns Bank area and subsequent number of recaptures would tend to overshadow recaptures from small-scale releases. Therefore all recaptures for this part of the analysis were standardized to the equivalent number of recaptures from 1000 releases.

Seasonal effects of cod movements were evaluated for the two Browns Bank and Georges Bank release sites. Recaptures from these sites were aggregated by quarter with recaptures in the first month after release excluded. Results were summarized by unit area within the release division.

To evaluate temporal effects, data were partitioned into groups representing recaptures from 0–12 months, >12 months after release, and total recaptures. The influence of size at release was also investigated but initial examination showed no substantial difference in either direction or distance among size groups. This may be due to the fact that most fish were greater than the L_{50} mature reported by Hunt (1996) for Georges Bank cod at the time of release and would be expected to diminish the potential impact of size on movement.

Recapture information that included latitude and longitude was used to summarize the tag recoveries by 10-min latitude and longitude squares for the Browns and Georges Bank release sites. Recaptures in each square were weighted by the adjustment factor index associated with the unit area in which the square was located. The Browns Bank and Georges Bank areas support substantial commercial fisheries and are thought to be centers of spawning activity. Tag releases were made during the spawning season and therefore recoveries should represent movement of postspawning fish.

The minimum, maximum, and average time at large after tagging was calculated for releases from each unit area. For recaptures with latitude and longitude location, the straight line distance between release and recapture site was calculated to determine the minimum, maximum. and average distance travelled.

A small proportion of recaptures included size at the time of recapture and these were used to estimate individual specific growth rates. The increase in length between release and recapture was adjusted to an annual value ((increment × 365)/days at large)

for each fish and averaged by 10-cm intervals of release length to give an annual growth rate.

Results

Average cod catches per tow, derived from U.S. spring and fall research surveys for 1982–91, are shown in Figure 2, A and B, and indicate widespread distribution throughout the area with some apparent centers of aggregation associated with banks. Densities and distributions show seasonal variation between the spring and fall. In the spring, distribution (with localized areas of high density) appears to be contiguous from Cape Cod, across Georges Bank, to Browns Bank and then farther east and west to the Bay of Fundy. In the fall, densities are lower and there is more apparent geographic isolation. Gavaris et al. (1993) found similar results when comparing seasonal distributions in relation to the IMB line in the Georges Bank area. The central part of the Gulf of Maine area has relatively low densities for both spring and fall seasons.

Over 58,000 releases were included in our study of which about 22,300 were in the Gulf of Maine primary study area. The release sites in the Gulf of Maine area, aggregated by ten-min latitude and longitude squares, are shown in Figure 1 and summarized by date and unit area in Table 1. Releases by area ranged from about 11,000 in 4Xp (Browns Bank) to only seven in 5Yd. Total recaptures were more than 6300 with over 2400 from the Gulf of Maine. Return rate by area varied between 0% and 34% with an average of 9%. Release length ranged from about 15 cm to about 140 cm. A relatively high proportion of released fish were >80 cm in the 5Zj area. The majority of released cod were larger than the L_{50} maturity (~43 cm; see Hunt 1996), with the exception of unit areas 4Xm and 4Xo.

Observed numbers of recaptures by division of release and recapture for each of "east of 4X," 4X, 5Y, and 5Z areas are shown in Figure 3. Over 97% of cod recaptured from releases east of 4X were also recovered east of 4X and, conversely, 74% of fish recaptured in this area originated from releases east of 4X. Further analysis of information on the area east of 4X is required but, in general, movement between this area and the Gulf of Maine appears to be limited. For division 4X, 80% of recaptures from releases in 4X occurred in 4X, with 8% moving east of 4X and 12% west to 5Z and 5Y. Of the total recaptures taken in 4X, 50% were from 4X releases, 42% from 5Y releases, and 8% from division 5Z releases. In division 5Y, 63% of recaptures from releases in 5Y occurred in 4X and of these only 21% occurred in 5Y and 2% from 5Z. However, of the total recaptures in 5Y, over 80% were from 5Y releases and 17% from 4X. The high proportion of recaptures in 5Y from division 4X is probably influenced by the small numbers of releases and recaptures as well as the distribution of commercial fishing in the vicinity of the 4X and 5Y boundary. Clark (1996) noted that Canadian land-

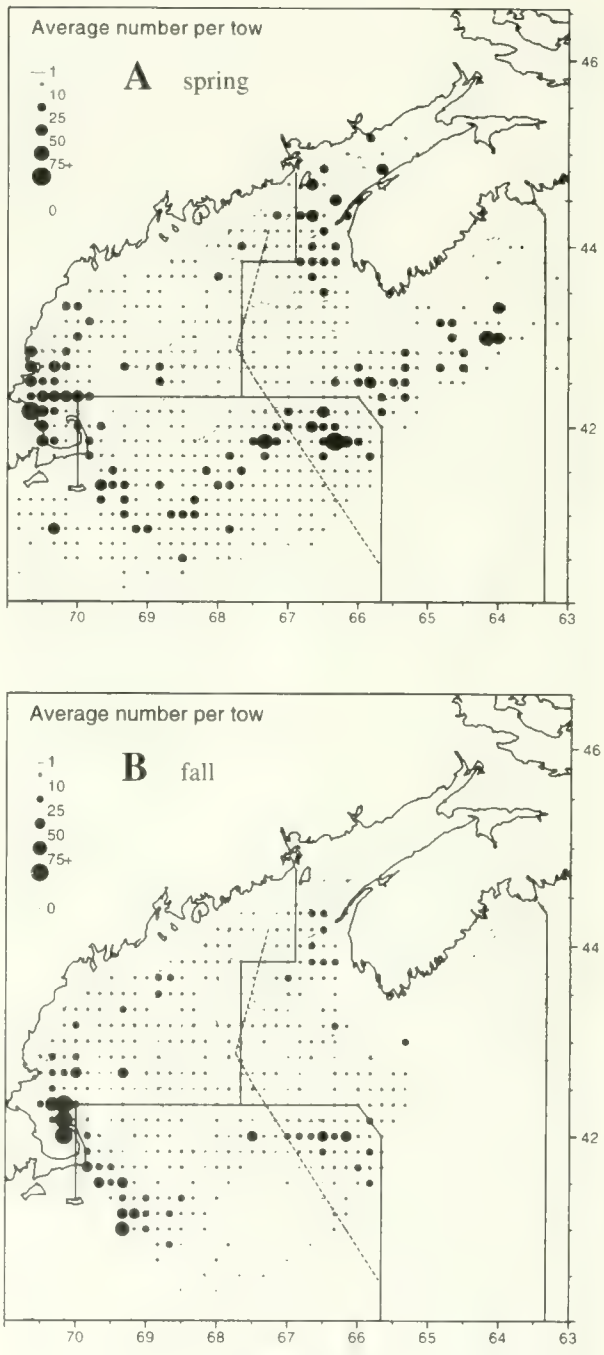

Figure 2

Mean catch per tow of cod derived from 1982–91 U.S. research surveys in the Gulf of Maine area: (**A**) spring and (**B**) fall.

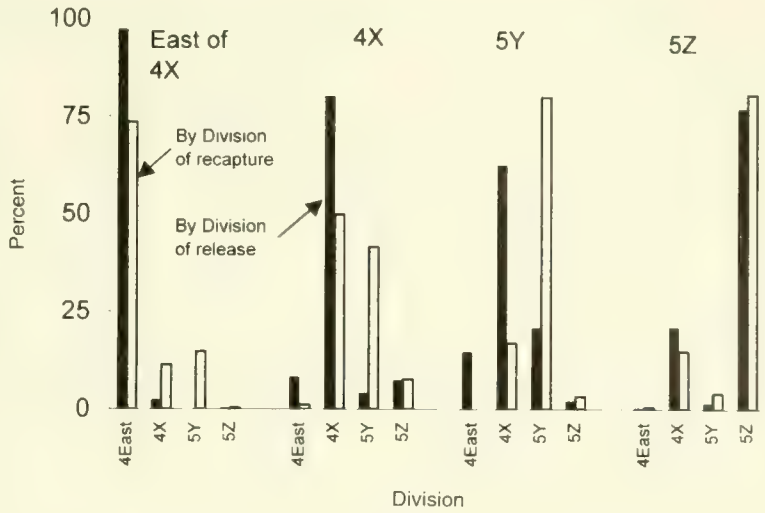

Figure 3

Percent of cod tag recoveries by NAFO Division of release (solid bar) and Division of recapture (pattern bar, based on 1000 releases) for divisions 4X, 5Y, 5Z, and the area east of 4X.

ings from the 5Y area near the 4X-5Y boundary are considered part of the 4X fishery and therefore were included in our 4X stock assessment. In division 5Z, 77% of cod released in 5Z were recaptured in 5Z and 21% were recaptured in 4X. Of the total recaptures in division 5Z, 81% were from 5Z releases and most of the movement out of the area occurred to the northeast (15%), towards division 4X.

The annual percent exploitation rate of cod by management area (4X, 5Y, 5Z) is summarized in Figure 4 for the 1980–97 time period. Reported landings by unit area showed considerable variation but proportions were relatively stable over time. In division 4X, unit area 4Xo accounted for about 38% of the 1980–97 total landings and unit area 5Yd for about 40% of the 5Y total. In subdivision 5Ze, unit areas 5Zg (30%) and 5Zj (40%) dominated, representing the U.S. and Canadian fisheries, respectively. The derived recapture adjustment factors, standardized to a maximum of 1.00, are given in Table 2 for each year and unit area. Annual factors ranged from 0.02 to 1.00, meaning that about 100 recaptures from a unit area with high landings and exploitation were proportionally equivalent to about two recaptures from a unit area with low landings and exploitation rate.

The effect of weighting tag recoveries to account for fishing effort is shown in Figure 5 for releases in the Browns Bank area. Weighted recoveries decrease the apparent extent of movement to 4Xo and 5Zj, because of their relatively high landings and exploitation rates, and increases the contribution of 4Xp recoveries. Similar effects are seen for other unit areas.

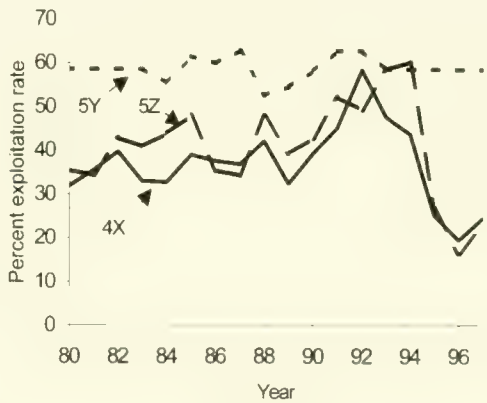

Figure 4

Reported percent exploitation rate of cod by the commercial fishery in management areas 4X, 5Y, and 5Z for 1980–97.

Table 3 provides a detailed summary of recaptures by unit area of release and recapture partitioned into <12 months elapsed time from release and the total number of recaptures. The observed number of tag returns, the number adjusted by unit area landings, and the percent of total adjusted number are shown. The percent of recaptures reported is based on only those released and recaptured in the Gulf of Maine

area. Table 3 summarizes results by area of release and shows the pattern of movement away from the release site (or no movement when the area of release=area recapture). Table 3 shows the pattern of movement into an area from standardized releases in adjacent areas and is organized so that the two aspects of tag recoveries appear on the same horizontal line. For example, in the second row of data, results show 31.4% of cod released in 4Xm were recaptured in 4Xo, whereas only 15.5% of cod recaptured in 4Xm originated from 4Xo releases.

About 63% of the cod tagged in 4Xm appeared to remain in the area although there was some movement to the west into adjacent areas. Over 76% of cod recaptured in 4Xm originated from 4Xm releases. At the divisional level, movement in relation to the division 4X/4W boundary is small (Fig. 3); however, exchange between divisions does occur and is concentrated in the 4Xm, 4Xn, and 4Xo areas.

No releases were made in 4Xn but about 80 recaptures were taken in the area. Most of these recaptures were from the Browns Bank (46%) and Georges Bank (27%) releases. Additional recaptures originated in the Bay of Fundy area and about 4% from the area east of 4X.

Results for the 4Xo area indicate a contrast between the two analyses of recaptures. Close to 100% of recaptures of cod released in the 4Xo area were

Table 1

Summary of cod tag releases and recaptures in NAFO divisions by release date. * indicates release from commercial fishing vessels.

Area released	East of 4X	4Xm	4Xo	4Xp	4Xq	4Xr	4Xs	5Yb	5Yc	5Yd	5Zj	5Zm	5Zo
Date	1978–81	Feb 80	May 79	Feb 84	Dec 94*	Jun 79	Aug 84	Jul 85	Jun 94*	Jul 94*	Feb 84	Mar 94	Jul 94*
N	36,338	808	694	3,980	50	141	67	350	27	7	1988	843	100
Length range (cm)	15–135	13–92	21–87	33–140	36–64	22–75	38–100	33–112	34–47	36–43	16–136	31–130	35–48
Mean length (cm)	48.8	47.9	41.9	71.9	47.4	36.7	57.1	59.9	41.1	40.3	61.2	69.9	42.4
Date				Mar 84	May 94*	Jul 85	Dec 85				Mar 85	Jun 94*	
N				786	4	216	73				500	266	
Length range				40–126	38–57	28–103	26–64				33–139	30–50	
Mean length				66.3	43.5	52.9	42				72.1	44.4	
Date				Feb 85	Dec 95*		Jul 85				Mar 94		
N				1,621	9		1399				3608		
Length range				38–142	38–72		26–94				30–144		
Mean length				79.8	48.1		52.6				73.8		
Date				Mar 85	May 96*		Nov 85						
N				4363	58		281						
Length range				32–140	39–85		28–87						
Mean length				72.9	58.8		48.9						
Date					Nov 96*		Jan 85						
N					17		4						
Length range					39–72		36–56						
Mean length					53.8		42.3						
Date							Jul 94*						
N							21						
Length range							36–47						
Mean length							40.3						
Total released	36,338	808	694	10,750	138	357	1845	350	27	7	6096	1109	100
Total recaptures	3883	100	237	1346	1	57	139	49	0	0	476	29	0
Percent recaptures	10.7	12.4	34.1	12.5	0.7	16.0	7.5	14.0	0.0	0.0	7.8	2.6	0.0

recaptured in 4Xo. Cod tagged in 4Xo were from an inshore area and may have been part of a local resident population. About 90% of tags recovered in 4Xo were from fish released in 4Xo and additional small contributions were from other Gulf of Maine locations.

The largest number of releases was from the Browns Bank area and results indicate a widespread dispersal within the Gulf of Maine. The majority of recaptures were from division 4X; substantial numbers of cod moved to the inner Bay of Fundy and smaller numbers moved east to 4Xn and 4Xo. About 33% of cod released in 4Xp were recaptured in the same area. Movement into Divisions 5Y and 5Z accounted for about 15% of the total releases. Of cod recaptured in 4Xp, about 50% originated from the same area, 27% from 5Yb, and about 11% originated from the Georges Bank area. Differences between immigration and emigration distributions may be due to seasonal patterns and commercial fishing operations. The Browns Bank area has been closed to commercial fishing during the winter spawning season and there is a low probability of capture during this time. Cod recaptured during the summer–fall fishing season may represent postspawning dispersal patterns.

In 4Xq, all three of the recaptures were taken in 4Xo. However, cod caught in 4Xq appeared to originate from diverse locations including 39% from 5Yb, 28% from Browns Bank, 20% from the inner Bay of Fundy, and 10% from Georges Bank.

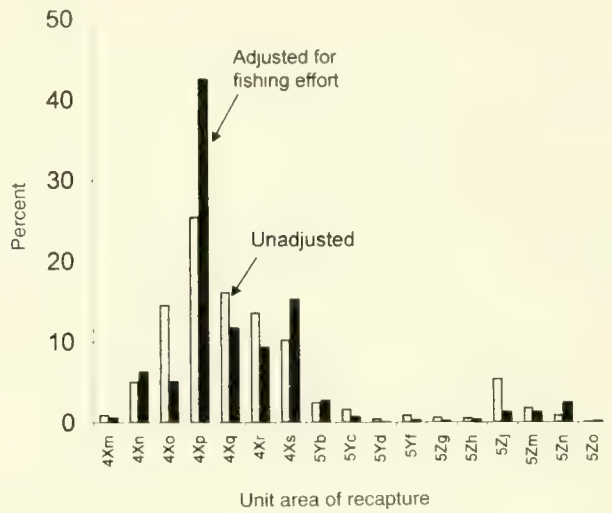

Figure 5

Comparison of percent recaptures by unit areas for Browns Bank releases using observed and effort-adjusted tag recoveries.

Unit area 4Xs and 4Xr represent the inner Bay of Fundy region. Movement of cod appears to occur into and out of the region as well as across the Bay from the Nova Scotia to New Brunswick sides. Over 75% of recaptured cod released in these areas were re-

Table 2

Annual adjustment factors by year and area used to prorate recoveries for probability of recapture, standardized to 1.00 for the area and year (5Zn, 1987) with the lowest landings and exploitation rate.

Area	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	Mean
4Xm	0.13	0.13	0.10	0.16	0.20	0.10	0.10	0.10	0.13	0.24	0.17	0.14	0.14	0.14	0.19	0.71	0.84	0.67	0.24
4Xn	0.21	0.28	0.18	0.32	0.20	0.25	0.17	0.17	0.18	0.32	0.41	0.22	0.12	0.12	0.28	0.30	0.47	0.36	0.25
4Xo	0.07	0.05	0.05	0.06	0.07	0.06	0.06	0.06	0.04	0.06	0.04	0.04	0.02	0.04	0.04	0.12	0.14	0.14	0.06
4Xp	0.44	0.33	0.25	0.22	0.27	0.29	0.54	0.24	0.15	0.12	0.18	0.14	0.15	0.14	0.14	0.13	0.25	0.23	0.23
4Xq	0.19	0.24	0.14	0.16	0.15	0.12	0.11	0.12	0.12	0.17	0.12	0.13	0.08	0.10	0.11	0.16	0.24	0.17	0.15
4Xr	0.15	0.12	0.11	0.13	0.12	0.11	0.13	0.23	0.21	0.24	0.16	0.09	0.07	0.08	0.10	0.21	0.24	0.14	0.15
4Xs	0.30	0.30	0.27	0.34	0.36	0.23	0.23	0.28	0.28	0.46	0.23	0.15	0.16	0.15	0.21	0.50	0.43	0.28	0.29
5Zg	0.04	0.05	0.04	0.05	0.05	0.04	0.07	0.08	0.05	0.05	0.05	0.04	0.06	0.04	0.03	0.06	0.11	0.08	0.06
5Zh	0.14	0.16	0.16	0.12	0.13	0.12	0.25	0.16	0.10	0.15	0.20	0.13	0.14	0.08	0.08	0.17	0.33	0.24	0.16
5Zj	0.08	0.06	0.04	0.04	0.05	0.04	0.05	0.04	0.03	0.05	0.04	0.03	0.02	0.02	0.03	0.20	0.23	0.12	0.06
5Zm	0.33	0.26	0.23	0.23	0.10	0.10	0.13	0.22	0.10	0.13	0.15	0.11	0.12	0.08	0.11	0.32	0.55	0.62	0.22
5Zn	0.39	0.40	0.71	0.97	0.28	0.38	0.79	1.00	0.57	0.53	0.32	0.21	0.34	0.19	0.15	0.33	0.64	0.46	0.48
5Zo	0.49	0.76	0.44	0.38	0.29	0.22	0.32	0.78	0.34	0.40	0.32	0.27	0.46	0.33	0.18	0.41	0.79	0.57	0.43
5Yb	0.61	0.76	0.41	0.31	0.30	0.15	0.19	0.13	0.33	0.44	0.28	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.24
5Yc	0.15	0.15	0.10	0.11	0.10	0.08	0.06	0.06	0.13	0.07	0.07	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.09
5Yd	0.02	0.02	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
5Ye	0.02	0.02	0.02	0.02	0.03	0.03	0.04	0.05	0.04	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
5Yf	0.12	0.09	0.07	0.09	0.08	0.05	0.06	0.05	0.12	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.08

Table 3

Summary of cod tag recaptures ordered by area of release and area of recapture (per thousand).

		<12 months total			Total					<12 months total			Total		
Release area	Recapture area	Number recaptured	Adjusted number	Percent	Number recaptured	Adjusted number	Percent	Recapture area	Release area	Number recaptured	Adjusted number	Percent	Recapture recaptured	Release number	Percent
4Xm	4Xm	14	52	55.4	25	92	63.4	4Xm	4Xm	17.2	69.0	73.1	30.7	120.7	76.9
	4Xo	4	37	39.2	5	46	31.4		4Xo	4.3	18.5	19.7	5.7	24.4	15.5
	4Xp	1	2	2.5	2	5	3.2		4Xp	0.6	2.4	2.5	1.0	4.1	2.6
	4Xq	1	3	2.9	1	3	1.9		4Xq						
									4Xs				0.5	2.5	1.6
									5Zj	0.4	3.5	3.7	0.4	3.5	2.2
								4Xn	4Xp	3.5	25.4	35.0	5.6	41.3	45.6
									4Xr	2.8	17.6	24.3	2.8	17.6	19.5
									4Xs	0.5	3.4	4.7	0.5	3.4	3.8
									5Zj	0.9	8.3	11.4	0.9	8.3	9.1
									5Zm	1.2	16.6	22.9	1.2	16.6	18.3
4Xo	4Xm	3	11	0.6	4	15	0.7	4Xo	4Xm	4.9	66.3	1.6	6.1	76.4	1.7
	4Xo	217	1981	99.4	228	2082	98.8		4Xo	316.1	3840.8	92.0	328.0	3990.9	89.7
									4Xp	11.1	107.0	2.6	16.0	169.0	3.8
									4Xq	18.5	116.7	2.8	18.5	116.7	2.6
									4Xs	0.5	11.1	0.3	0.5	11.1	0.2
									5Yb				2.9	25.7	0.6
	5Zj				1	10	0.5		5Zj	3.9	32.4	0.8	5.0	47.7	1.1
4Xp	4Xm	6	32	0.7	11	58	0.7	4Xp	4Xm	2.5	28.8	9.7	2.5	28.8	5.0
	4Xn	36	302	6.5	60	512	6.5		4Xn						
	4Xo	119	255	5.5	173	379	4.8		4Xo						
	4Xp	159	1304	28.2	305	2542	32.5		4Xp	15.7	163.2	54.8	28.0	290.5	50.3
	4Xq	123	878	19.0	191	1371	17.5		4Xq						
	4Xr	123	907	19.6	161	1192	15.2		4Xr						
	4Xs	68	602	13.0	121	1082	13.8		4Xs	0.5	11.1	3.7	3.8	33.9	5.9
	5Yb	18	57	1.2	29	92	1.2		5Yb	2.9	58.3	19.6	11.4	158.0	27.4
	5Yc	17	60	1.3	19	67	0.9		5Yc						
	5Yd	1	1	0.0	4	4	0.1		5Yd						
	5Yf	8	26	0.6	10	33	0.4		5Yf						
	5Yg	1	2	0.0	1	2	0.0		5Yg						
	5Yu				1				5Yu						
	5Zg	4	9	0.2	7	15	0.2		5Zg						
	5Zh	5	30	0.6	6	36	0.5		5Zh						
	5Zj	35	62	1.3	64	114	1.5		5Zj	3.5	28.1	9.4	5.4	41.7	7.2
	5Zm	8	42	0.9	21	116	1.5		5Zm	1.2	8.3	2.8	3.6	23.3	4.0
	5Zn	3	62	1.3	10	202	2.6		5Zn						
	5Zo				1	16	0.2		5Zo						
4Xq	4Xo	1	3	100.0	1	3	100.0	4Xq	4Xo						

continued

Table 3 (continued)

Release area	Recapture area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Number recaptured	Total: Adjusted number	Total: Percent
4Xr	4Xn	1	9	5.9	1	9	4.7
	4Xp						
	4Xq	3	22	15.0	3	22	12.0
	4Xr	25	84	58.9	33	115	64.1
	4Xs	9	20	13.7	10	22	12.1
	5Yb	3	9	6.5	3	9	5.2
	5Yf				1	3	1.8
4Xs	4Xm				1	6	0.7
	4Xn	1	9	1.9	1	9	1.1
	4Xo	1	2	0.5	1	2	0.3
	4Xp	1	8	1.8	7	62	7.8
	4Xq	5	36	7.8	9	65	8.3
	4Xr	24	177	38.7	30	221	28.1
	4Xs	21	186	40.8	42	376	47.7
	5Yb	7	22	4.7	8	25	3.1
	5Yf				1	3	0.4
	5Zj				1	2	0.3
	5Zm	3	17	3.8	3	17	2.2
5Yb	4Xo				1	2	0.9
	4Xp	1	8	4.5	4	34	13.2
	4Xq	7	49	26.6	9	64	24.6
	4Xr	12	88	47.7	12	88	34.0
	4Xs	1	9	4.7	4	36	13.7
	5Yb	9	27	14.6	9	27	10.4
	5Yc	1	4	1.9	1	4	1.4
	5Zm				1	5	1.8

Recapture area	Release area	Total: Number recaptured	Total: Adjusted number	Total: Percent	<12 months total: Recapture recaptured	<12 months total: Release number	<12 months total: Percent
	4Xm	1.2	7.2	3.7	1.2	7.2	2.7
	4Xp	11.9	50.7	25.7	17.7	75.7	28.0
	4Xr	8.4	34.7	17.6	8.4	34.7	12.9
	4Xs	2.7	11.1	5.6	4.9	20.9	7.7
	5Yb	20.0	77.4	39.2	25.7	104.3	38.6
	5Zj	3.3	16.1	8.1	4.8	27.0	10.0
4Xr	4Xn						
	4Xp	11.4	42.2	7.2	14.9	60.9	9.1
	4Xq						
	4Xr	81.2	351.5	59.8	92.4	400.3	59.8
	4Xs	13.5	53.9	9.2	16.3	66.2	9.9
	5Yb	34.3	138.6	23.6	34.3	138.6	20.7
	5Yf						
	5Zj	0.2	0.9	0.6	0.6	2.4	0.4
4Xs	4Xm						
	4Xn						
	4Xo						
	4Xp	6.3	56.8	10.1	11.2	100.9	14.6
	4Xq						
	4Xr	25.2	259.7	46.0	28.0	285.4	41.3
	4Xs	17.3	137.1	24.3	22.8	191.1	27.7
	5Yb	11.4	107.4	19.0	11.4	107.4	15.5
	5Yf						
	5Zj	0.4	3.9	0.7	0.6	5.8	0.8
	5Zm						
5Yb	4Xo						
	4Xp	1.7	13.7	4.1	2.7	22.5	6.5
	4Xq						
	4Xr	8.4	114.6	34.5	8.4	114.6	33.1
	4Xs	3.8	26.7	8.0	4.3	31.5	9.1
	5Yb	25.7	162.0	48.8	25.7	162.0	46.8
	5Yc						
	5Zm	1.2	15.3	4.6	1.2	15.3	4.4
5Yc	4Xp	1.6	5.1	36.6	1.8	5.7	39.1
	5Yb	2.9	8.9	63.3	2.9	8.9	60.7
5Yd	4Xp	0.1	0.1	30.9	0.4	0.4	50.0
	5Zj	0.2	0.2	61.6	0.4	0.4	50.0
5Ye	5Zj	0.2	0.2	100.0	0.2	0.2	100.0
5Yf	4Xp	0.7	1.8	74.5	0.9	2.3	21.3
	4Xr				2.8	6.4	60.2

continued

Table 3 (continued)

Release area	Recapture area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Number recaptured	Total: Adjusted number	Total: Percent
5Zj	4Xm	2	10	1.1	2	10	0.7
	4Xn	5	41	4.7	5	41	2.9
	4Xo	21	43	4.9	27	58	4.0
	4Xp	17	136	15.6	29	248	17.3
	4Xq	18	121	13.9	26	193	13.5
	4Xr	1	7	0.8	3	22	1.5
	4Xs	2	17	1.9	3	27	1.9
	5Yd	1	1	0.1	2	2	0.1
	5Ye	1	2	0.2	1	2	0.1
	5Yf	1	3	0.4	1	3	0.2
	5Zg	1	3	0.3	1	3	0.2
	5Zh	3	19	2.2	3	19	1.3
	5Zj	206	387	44.5	325	609	42.6
	5Zm	15	82	9.4	18	100	7.0
	5Zn				5	95	6.7
5Zm	4Xn	1	8	12.0	1	8	8.5
	4Xp	1	8	11.6	3	29	31.7
	4Xs						
	5Yb	1	3	5.0	1	3	3.6
	5Zg				1	6	6.0
	5Zj	23	46	71.3	23	46	50.3

Recapture area	Release area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Recapture recaptured	Total: Release number	Total: Percent
	4Xs				0.5	1.4	12.7
	5Zj	0.2	0.6	27.0	0.2	0.6	6.0
5Zg	4Xp	0.4	0.7	47.0	0.6	1.2	8.3
	5Zj	0.2	0.8	51.8	0.2	0.8	5.5
	5Zm				1.2	12.1	85.8
5Zh	4Xp	0.5	2.4	41.3	0.6	2.9	45.5
	5Zj	0.6	3.5	59.2	0.6	3.5	54.6
5Zj	4Xm						
	4Xn						
	4Xo				1.4	3.2	1.8
	4Xp	3.2	6.1	4.8	5.9	11.0	6.2
	4Xq						
	4Xr						
	4Xs				0.5	1.0	0.6
	5Yd						
	5Ye						
	5Yf						
	5Zg						
	5Zh						
	5Zj	39.6	72.2	56.6	60.1	112.0	63.3
	5Zm	27.3	49.1	38.5	37.3	49.1	27.8
	5Zn						
5Zm	4Xn						
	4Xp	0.7	3.4	7.2	1.9	12.6	20.9
	4Xs	1.6	15.0	31.4	1.6	15.0	24.8
	5Yb	2.9	14.0	29.4	2.9	14.0	23.3
	5Zg						
	5Zj	3.0	15.2	31.9	3.3	18.6	30.9
5Zn	4Xp	0.4	4.2	62.4	0.9	12.1	56.4
	5Zj	0.2	2.5	37.3	0.9	9.3	43.4
5Zo	4Xp				1.0	16.0	99.9

covered there and between 15% and 20% of recaptures were from releases in the 5Yb area. Cod tagged in unit area 4Xs show more widespread dispersal than those from 4Xr.

The small number of releases from division 5Y precluded detailed interpretation of movement. However, there is an indication of association with the 4X area, as well as movement from the Browns Bank area into 5Y, both of which were not unexpected because the majority of releases were near the northeastern border of 5Y. Results, therefore, probably do not reflect those for the remainder of the 5Y area.

The pattern observed for Georges Bank is similar to that seen on Browns Bank. Dispersal of postspawning cod appears to be substantial in both a north and south direction. Interaction between the Browns Bank and inshore area and Georges Bank accounted for most of the movement of tagged cod. The interchange was bidirectional, but more cod appeared to move from Georges Bank to Browns Bank (about 30%) compared with about 3% of Browns Bank cod moving to Georges Bank. Relatively small numbers of cod released in the 5Zj and 5Zm area were recaptured in areas further to the south or west. However, Hunt and Buzeta (1996) noted that the U.S. commercial fishery, and therefore the probability of recovering tags from the 1994 and later releases in the area west of the IMB, has been substantially reduced with the introduction of closed areas in 1995.

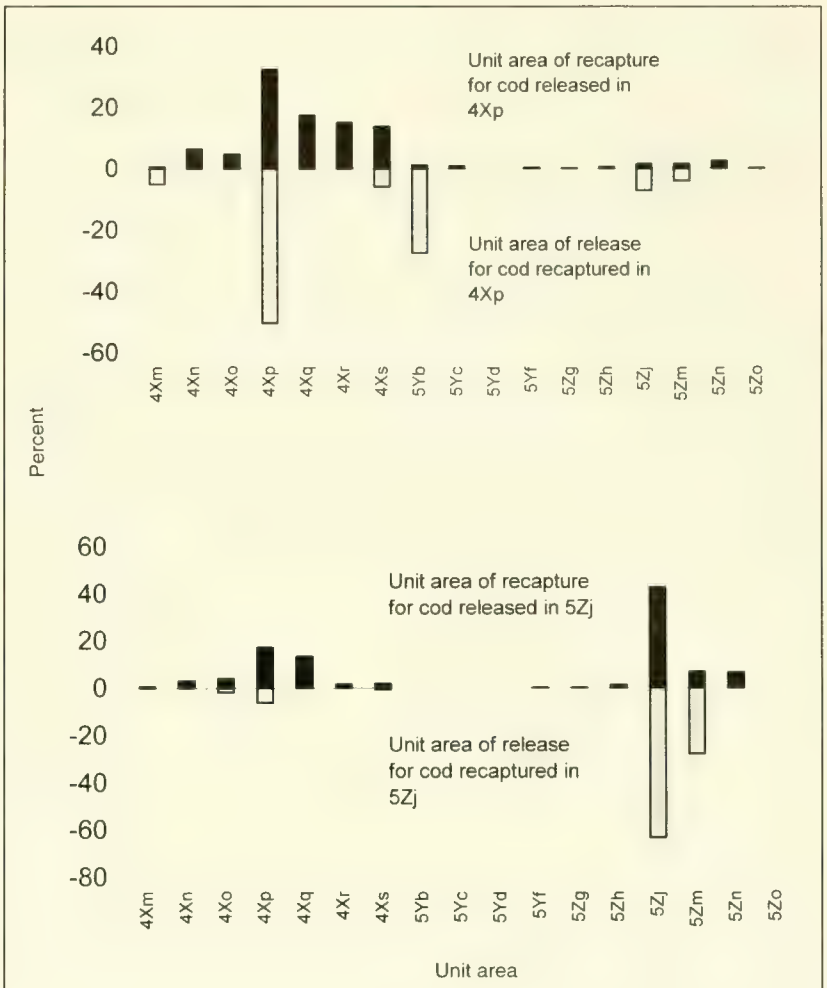

Figure 6

Summary of adjusted cod tag recoveries for the Browns Bank (4Xp) and Georges Bank (5Zj) areas, aggregated by unit area.

Information for the Browns Bank and Georges Bank areas is shown in Figure 6 for adjusted recaptures in the area and from the area. Preliminary comparison of recoveries in the first twelve months and total recoveries showed little variation in the distribution or proportions (Table 3) and therefore total recoveries were used. Dispersal from the area of release appears to be substantial for both the 4Xp and 5Zj areas. However, a high proportion of fish recaptured in the two areas was released from the same area. The two patterns may represent postspawning dispersal (top panel for each area) and summer distribution or year-round residents (bottom panel for each area).

The seasonal distribution of recaptures from the Browns Bank and Georges Bank areas is shown in Figure 7. Recaptures were combined by quarter and unit area (by division for recaptures outside the division of release). In the Browns Bank area, seasonal distribution appears to be consistent with aggregation in the spawning season (first quarter) and with progressive dispersal to adjacent areas in the remainder of the year. This pattern may be repeated on an annual basis with return of migrants during the spawning season. Seasonal trends in the Georges Bank area are more difficult to interpret and the influence of fishing season may be a factor, compared with trends for Browns Bank, because closure to commercial groundfishing in the first half of the year limits potential recoveries during the spawning season. However, the recapture pattern for cod recovered in division 4X suggests that the migrants do not return to Georges Bank because the proportion remains relatively constant over the first to third quarters and increases in the fourth quarter.

Figures 8 and 9 provide information on the spatial dispersal of cod tagged in the Browns Bank and Georges Bank areas with adjusted recoveries aggregated by 10-min squares and expressed on a per thousand basis. Most recoveries were made near the respective release site. When movement occurred, a general pattern of dispersal from the release site with a gradient from the tagging site to the edges of the distribution was evident. Intermediate areas of aggregation were consistent with the geographic distribution of fisheries effort and associated probability of recapture. Interchange occurred between release site areas, but the main vector of movement from both sites was towards the northeast. As a result, most long distance recoveries were made in the southwestern Nova Scotia and Bay of Fundy inshore areas, although there was limited movement into the northwestern Gulf of Maine or western Georges Bank areas.

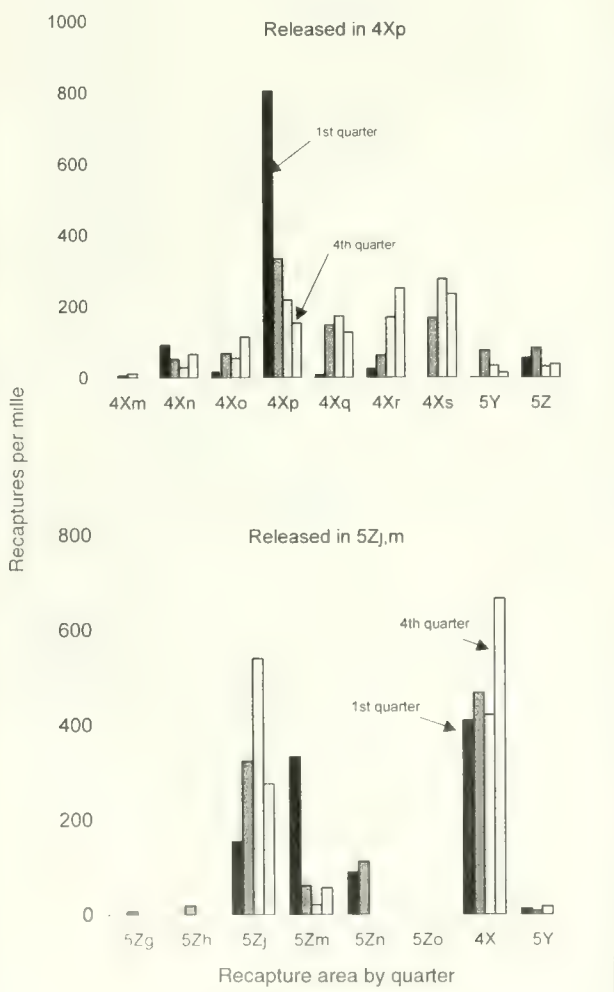

Figure 7

Quarterly distribution of cod tag recoveries from the Browns Bank (4Xp) and Georges Bank (5Zj) release areas, aggregated by unit area.

The two time periods associated with Georges Bank tagging are compared in Figure 10 for the 1994 and 1984–85 experiments. The two distributions are similar and both show the majority of cod remaining near the release area; more of the long distance dispersion occurred into the 4X area than to the west into the inner Gulf of Maine. Similarity in the results from the two time periods indicates some consistency in the northeast vector of movement. However, a higher proportion of cod were recaptured in 4X from the 1994 experiment (55%) compared with the earlier releases (42%). As noted above, the reduced U.S. commercial fishery in the area west of the IMB since 1995 also reduced the probability of tag recaptures from the 1994 experiment in this area.

The distribution of recaptures and elapsed time for the February and March releases for unit areas 4Xp (Browns Bank) and 5Zj (Georges Bank) are shown in Figure 11. The majority of returns in both areas occurred in the first 24 months after release, and the maximum time at large was 87 months (Table 4), but the overall average of time at large was less than 8 months. Many fish were recaptured in the first month after release, probably before postspawning dispersion had occurred. Maximum distance travelled was over 620 km and the mean distanced travelled was 60 km. Substantial numbers of cod moved hundreds of kilometres, indicating that cod can survive the stress of tagging and are capable of long distance movements. A strong seasonal pattern, consistent with the seasonal nature of the commercial fishery, is evident. The fishery on Browns Bank is typically year round, with peaks late spring and summer (Clark, 1996), and on Georges Bank, the fishery typically opens in June (Hunt and Buzeta 1996). The seasonal peaks in recaptures (4–6, 16–18, etc. months after February releases) coincides with the commercial fishing activity.

Length at the time of recapture was available for a relatively small proportion of recaptures. For these samples, the net increase in length and elapsed time was used to calculate a specific growth rate, expressed as annual rate, for each unit area. Results are given in Table 5 for 10-cm length-at-release intervals but sample size was small for all but the 4Xp, 4Xs, and 5Zj areas. The calculated annual growth rates indicate differences between areas and follow an expected pattern of decrease as the length at release increases. Of these three areas, the Georges Bank area had the fastest growth with an annual increase of about 19 cm for cod released as 40-cm

individuals. Estimates of growth rates from this study are consistent with the more extensive study on cod growth completed by Shackell et al. (1997).

Discussion

Fisheries management objectives for either conservation or yield from a defined management unit are usually based on a closed system approach that requires that emigration and immigration of fish from adjacent stocks be sufficiently low so as to avoid confounding stock-status evaluations. Gulland's (1983) operational definition of a stock also considered interchange between stocks and he suggested that it can be ignored if conclusions on the population dynamics of the stock remain valid. Therefore, two problems require evaluation in assessing stock definitions: 1) Is there evidence of interchange of fish at a geographic scale larger than the one used to define a stock boundary? and 2) If interchange does occur, what are the impacts on population dynamics and on the assumptions used in models to estimate population parameters?

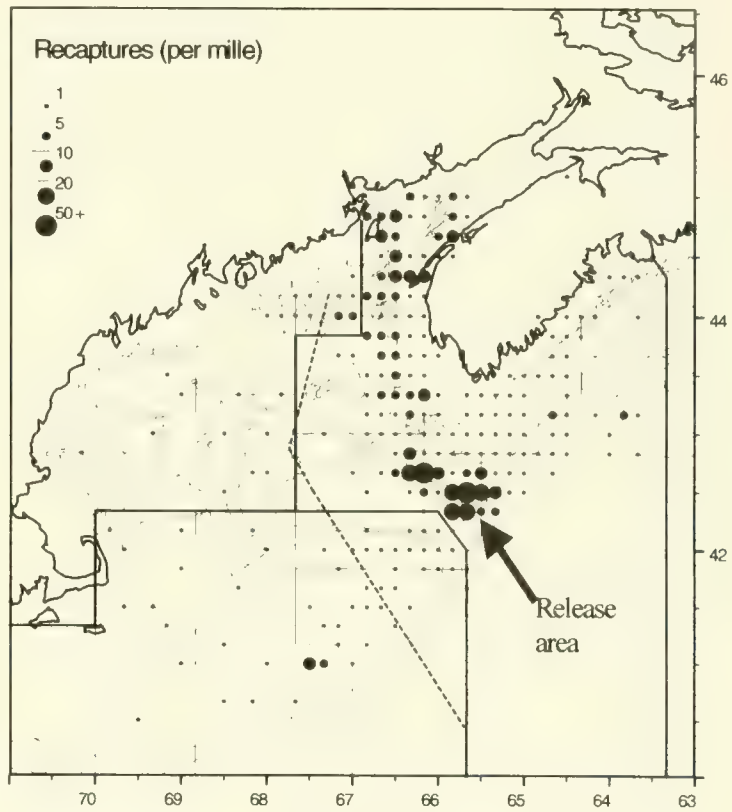

Figure 8
Distribution of adjusted cod tag recoveries from releases in the Browns Bank (4Xp) area, aggregated by 10-min latitude and longitude squares.

Tagging experiments can address the first of the two questions provided that the study logistics have not compromised the results and that both ongoing fisheries removals and management activities during the recapture period do not invalidate interpretation of the results. Capture, tagging, and release of cod with bottom trawl methods and T-bar tags can generate a large number of releases and, according to a relatively high recapture rate and extended time at large, appear to result in nominal tag- or stress-induced mortality. During the 1994 experiment, cod tagged from one tow were recaptured in a subsequent tow, either the same day or several days later and thus may indicate that tagged cod resume a normal schooling pattern shortly after release. Efficiency of the tagging operation is also a contributing factor as is the time of year, depth, and condition of tagged fish. Clay et al. (1989) reported on tagging experiments under winter conditions and concluded that cod at this time of year have a better chance of surviving the tagging process. Tag loss was not examined in our study but Saunders et al. (1990), in a study of sablefish tagged with tags similar to those used in our study, concluded that tag loss could be as high as 10% in the first year and 2% per year thereafter. Less than 10% of cod tagged with T-bar tags for identification in a live-fish holding facility experienced tag loss in the first week, although losses were higher after biweekly netting and sampling for length and weight observation (Nelson[1]).

In the present study, the influence of high annual mortality rates (Z), failure to report recaptures, and the effectiveness of advertisements and rewards, the impact of fishery controls, and the potential bias between Canada and U.S. reporting rates may be more substantial than factors such as tag loss. However, these variables are difficult to quantify.

All cod stocks in the study area have been subjected to very high exploitation rates in the last decade. For example, Hunt and Buzeta (1996) reported rates of over 40% in the 1990s for the Georges Bank cod stock. A similar capture rate applied to the tagged population [N] could result in an apparent rate [R] of over 20% returns after accounting for tagging mortality (~20%) and tag loss (~10%) and assuming full reporting [$R = 0.4(N - N(0.2 + 0.1) = 0.28N$]. Observed return rates were less than half those for the Georges Bank and Browns Bank areas and a lack of reporting could be a contributing factor. Anecdotal information from field staff working in fishing ports

[1] Nelson, C. 1996. Department of Fisheries and Oceans, St. Andrews, New Brunswick, Canada. Personal. commun.

indicates that some fishermen with tags did not return them because of resistance to identifying fishing locations and because of preconceived ideas and concerns about the significance of the release and recapture site. The extent of a lack of reporting is difficult to quantify and its effect may not introduce bias if nonreported tags have the same geographic distribution as reported tags.

Advertizing campaigns for the 1994 experiment were much more extensive than those used in the early 1980s. Printed notices covered a larger audience, the experiment was discussed with industry representatives and conducted with their support, interim results were presented, and a more active role was taken by field staff to collect recovered tags. However, the return rate was higher in the 1980s. For example, the return rate in the first 24 months for the 1984–85 Georges Bank experiments was about 12.2% compared with 5.5% for the 1994 experiment.

Fisheries management controls may play a more substantial role in determining the number of recaptures. Controls may include area closures, restricted seasons, and catch limitations. The Browns Bank area has been closed to fishing during the winter spawning season for many years. Canadian commercial fishing on Georges Bank has been closed between January and May since 1994, and the United States has an extensive closed area covering most of the northeast part of the Bank. These restrictions substantially reduce the possibility of recaptures during the spawning season.

The establishment of the International Maritime Boundary in 1984 between the United States and Canada and the associated opinions and concerns of the fishing industry have undoubtedly introduced bias in the tag return rate and perhaps in the reported recovery location. It might be assumed that the direction of the bias would tend to support the concept of national ownership of the resource by the fishing industry and that tags recovered at times or locations that appeared to contradict this opinion would be withheld or discarded. Comparison of tag recoveries from the 1984–85 releases with those from the 1994 releases does not show substantial differences in distribution of fish. The first period includes the time when response to international boundary change would have been most sensitive and pronounced. The second period, more than ten years after the change, might be expected to have reduced concerns by fishermen on tag location. However, the impact of nonreporting bias would be of most concern in evaluating the proportional spatial distribution of tag recoveries. Bias in reported recapture location is of less concern because fishing activities are monitored and there is limited opportunity to misreport the area of operations.

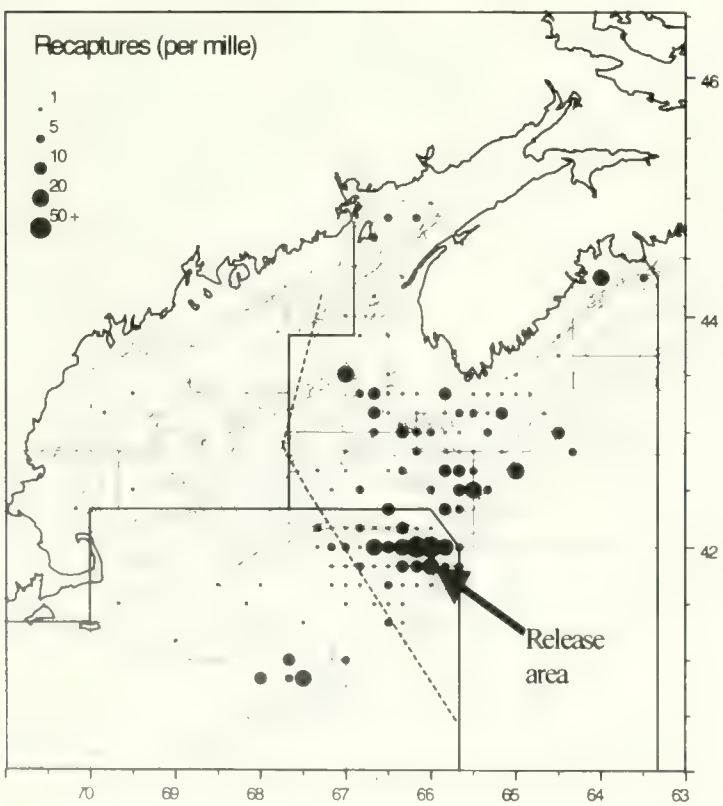

Figure 9

Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by 10-min latitude and longitude squares.

Total allowable catches and landings of cod from the Georges Bank area in 1994 declined to less than 50% of the recent ten-yr average and are expected to remain at low levels for a number of years (Hunt and Buzeta, 1996). The impact of reduced catches is accounted for, to some extent, by reduced annual exploitation and its impact on tag-recapture adjustment. However, other changes in the fishery, such as shifts in gear sectors and spatial redirection of effort, may offset this adjustment.

Even with the need, discussed above, to qualify the interpretation of tagging data, we believe the results of the present study clearly indicate that interchange between the 5Zj,m and 4X cod management units occurs with a net movement from 5Zj,m to 4X. Cod released on Georges Bank exhibited movement outside the 5Z management area onto Browns Bank and the inshore areas of Nova Scotia and the Bay of Fundy. Cod released on Browns Bank also moved to the inshore area of Nova Scotia

as well as onto Georges Bank. These results correspond to those of historical studies, although conclusions from the earlier studies may be more limited in scope owing to the smaller number of released fish and the lower intensity of commercial fisheries at the time. In his review of tagging results from the late 1890s to the 1960s in the Gulf of Maine, Wise (1963) concluded that cod of the offshore areas of Browns and Georges Banks were closely related to fish of the southwestern Nova Scotia area. Wise and Jensen (1960) had earlier concluded that the eastern Georges Bank cod population mixed little with the more western or southern components and interacted primarily with the southwestern Nova Scotia area. Templeman (1962) in summarizing cod tagging information for the northwest Atlantic concluded that there were discrete spawning stocks on the eastern part of Georges Bank and Browns Bank and mixing in both directions across the Fundian Channel as well as to inshore areas. Results of tagging studies completed in 1969 on Browns Bank and in 1972 from inshore areas of Nova Scotia were reported by Halliday (1973) and he concluded that there was a separation of inshore and offshore stocks. McKenzie (1956) and McCracken (1956) tagged cod in the inshore area of southwest Nova Scotia and observed limited interchange with the offshore banks and the Bay of Fundy. They concluded that the resident inshore cod stocks in the Bay of Fundy and southwestern Nova Scotia were relatively stationary. They also explained the offshore recaptures of cod tagged in the inshore area as evidence that cod from more migratory stocks could be present in inshore areas at certain times of the year.

Hunt and Buzeta (1989) provide details of the basis for partitioning the northeast part of Georges Bank (5Zj,m) as a separate Canadian management unit distinct from the remainder of the 5Zw+SA6 area. They concluded that spatial distribution from tagging studies and other biological characteristics were sufficiently distinct to define the 5Zj,m area as a management unit that could be expected to benefit from management controls. However, the 5Zj,m area is partitioned by the IMB so that commercial fisheries by Canada and the United States are limited to their respective sides. Gavaris et al. (1993) conducted an analysis of cod movement in relation to the IMB using commercial catches and research sur-

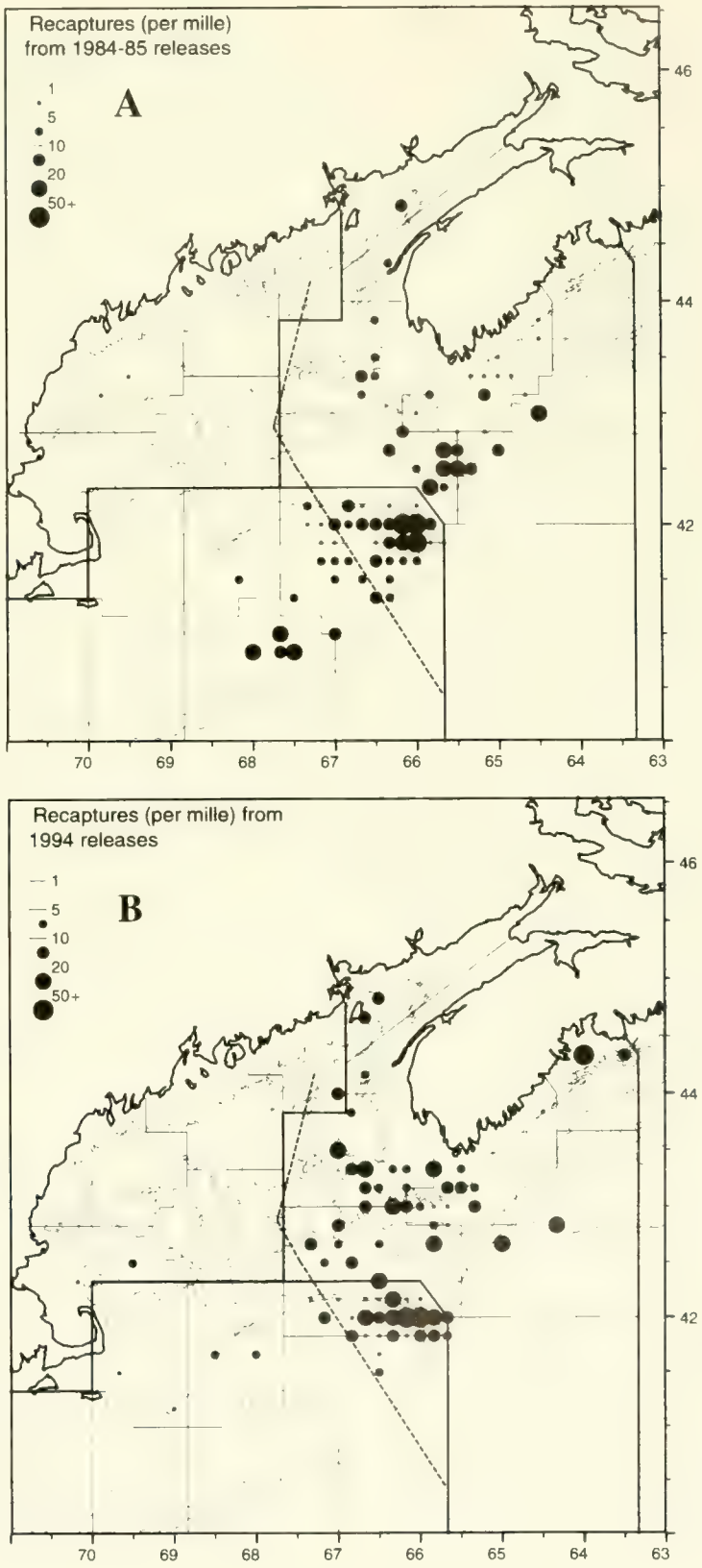

Figure 10

Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by 10-min latitude and longitude squares: (**A**) 1994 releases; (**B**) 1984–85 releases

Table 4

Summary by unit area of release of months after release to recapture and distance travelled (km).

Area of release	Months after release			Distance travelled		
	Minimum	Maximum	Average	Minimum	Maximum	Average
4Xm	0	87	12.0	1.1 2	385	64.5
4Xo	0	25	2.4	0	448	7.2
4Xp	0	62	12.2	2	626	128.6
4Xq	7	7	7	24	24	24.0
4Xr	0	28	4.4	0	235	25.4
4Xs	0	38	8.5	0	385	75.8
5Yb	0	31	7.0	2	221	66.5
5Zj	0	65	10.1	2	367	62.3
5Zm	3	16	5.3	22	265	93.4
Average	0	39.9	7.6	5.9	328.6	61.0

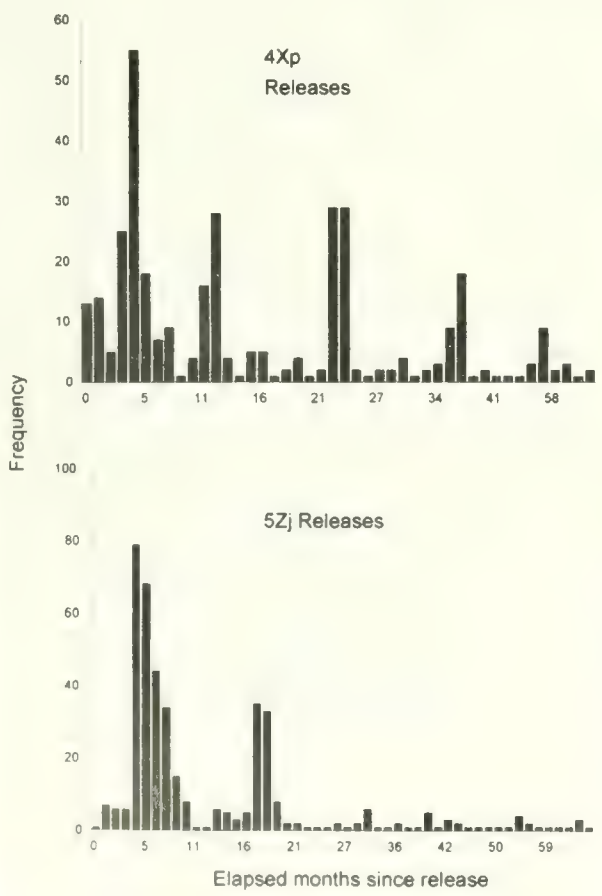

Figure 11

Summary of adjusted cod tag recoveries for releases in the Browns Bank (4Xp) and Georges Bank (5Zj) areas by elapsed time from release to recovery, in months.

vey indices. They concluded that extensive movement does occur with a strong seasonal pattern in which almost 100% of the biomass is on the Canadian side in the fall–winter period and about 65% in the spring–summer period. Results of the present study support the occurrence of seasonal movement but also indicate that it is not a closed system. There is evidence of immigration and emigration and an apparent net loss from the Georges Bank area to the Browns Bank and division 4X area.

In division 4X, two substocks (Bay of Fundy and Scotian Shelf) are already assumed (Clark, 1996) with distinct growth characteristics. However, tagging results show interchange between the Bay of Fundy, the inshore areas of southern Nova Scotia, and Browns and Georges Banks. The greatest exchange occurs between the offshore Browns Bank area and the inshore areas and the Bay of Fundy. Our results indicate that the extent of movement by cod in the Gulf of Maine area is substantial and that it crosses the present stock boundaries between 4X, 5Y, and 5Z. The interchange appears to be primarily between the eastern part of Georges Bank (the Canadian management unit) and 4X. Although movement between 4X and 5Y was observed, the number of releases and recaptures was small and the tagging location was close to the boundary between these areas. Exchange between 5Z and 5Y also occurs but at a relatively low rate.

Investigation of the potential impact of cod movement between stocks on models used for population estimates will require further work. Interpretation of diagnostics for population models such as ADAPT (Gavaris, 1988) from a stock concept might give

Table 5

Growth rate of cod estimated from net increase in length and elapsed time, expressed as an annual rate. Number of observations are shown in parentheses.

Release length (cm)	4Xm	4Xo	4Xp	4Xr	4Xs	5Yb	5Zj
20–29	12.5 (2)	12.0 (4)					
30–39	13.4 (7)	14.9 (6)		17.7 (8)	26.6 (4)		
40–49	7.9 (7)	8.9 (8)	12.4 (7)		15.8 (15)	33.8 (5)	18.9 (16)
50–59	10.7 (22)	8.0 (4)	9.2 (28)	2.6 (3)	15.8 (16)	30.7 (3)	16.9 (12)
60–69	5.1 (4)		7.5 (66)	18.0 (2)	10.8 (18)	18.9 (9)	12.2 (45)
70–79			6.7 (88)	6.0 (1)	4.8 (7)	21.0 (2)	11.9 (26)
80–89			5.7 (46)			4.0 (1)	7.2 (18)
90–99			3.7 (14)				5.8 (11)
100–109			3.1 (3)				6.9 (2)

some indication of the need for revising model formulations. For example, changes in apparent natural mortality or unexplained changes in fishing mortality could be evaluated as the result of losses due to emigration or increases due to immigration. However, stock definition may be further confounded if cod movements have a temporal element and shifts in distribution occur without permanent loss or gain.

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The authors express their appreciation to the many individuals who participated in the at-sea tagging operations and in particular to Francois D'Entrement, a fisherman who joined the 1994 survey. We also thank the individuals finding and returning tags for their interest and co-operation. Don Clark and Jay Burnett provided valuable comments on an earlier version of the manuscript. John Neilson provided many helpful suggestions from a fisheries management perspective. Suggestions from two anonymous reviewers improved the analysis and clarity of the report.

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Growth analysis of striped mullet, *Mugil cephalus*, and white mullet, *M. curema* (Pisces: Mugilidae), in the Gulf of Mexico

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Abstract.—The parameters from von Bertalanffy's growth equation were estimated for *Mugil cephalus* and *M. curema* located in Tamiahua coastal lagoon in Veracruz, México. Also differences in growth and longevity between sexes were obtained. The following were growth parameters for *M. cephalus*: L_∞ = 642.4 mm, W_∞ = 2,352.12 g, k = 0.099, t_0 = –2.85, $(A_{0.95})$ = 28.3 years; and for *M. curema*: L_∞ = 461.4 mm, W_∞ = 844.73 g, k = 0.14 y t_0 = 3.62, $(A_{0.95})$ = 18.7 years. Some important differences among growth rates from other areas were found. Significant differences in the growth rate between sexes were observed. The following were growth parameters for *M. cephalus*: females: L_∞ = 622.9 mm, k = 0.107, t_0 = –2.67; $A_{0.95}$ = 26.2 years; males: L_∞ = 603.9 mm, k = 0.105, t_0 = –2.98; $A_{0.95}$ = 26.5 years; for *M. curema*: females: L_∞ = 454.6 mm, k = 0.135, t_0 = –3.94; $A_{0.95}$ = 19.2 years; males: L_∞ = 411.8 mm, k = 0.187, t_0 = –3.03; $A_{0.95}$ = 14.0 years.

The striped mullet, *Mugil cephalus* (Linnaeus, 1758), has a worldwide distribution, between 42°N and 42°S (de Silva, 1980), whereas the white mullet, *Mugil curema* (Valenciennes, 1836), is basically an American species found from Cape Cod, USA, to Brazil in the Atlantic and from Bahia Magdalena, Mexico, to Chile in the Pacific (Jordan and Everman, 1896). However, Alvarez (1976) has recorded *M. curema* off the western coast of Africa.

In Mexico, 99% of the commercial catch of these mullets takes place in the states of Tamaulipas, mainly in Laguna Madre and in Veracruz, and mainly in the Pueblo Viejo and Tamiahua. The mullet fishery constitutes one of the ten most important fisheries in Mexico as a result of its catch volume, which surpasses 10,000 metric tons (t) annually (Polanco et al., 1987).

These species provide both the meat and the roe, locally called "hueva," which commands a greater commercial price than the meat. Whereas striped mullet meat has a value of one US$ per kg, the roe is valued at seven US$ per kg. The female gonad has a widespread market because it is eaten regionally as well as nationally and internationally. In 1995 alone, 43 t of roe with a value of US$ 150,000 (at the present time US$ 800,000) were exported to the United States (Polanco et al., 1987).

Although these species of mullets represent an important source of food in many countries, studies on their ecology and population dynamics are insufficient. In Mexico some population parameters of *M. cephalus* in Tamiahua lagoon, Veracruz, have been analyzed by Marquez (1974) and Garcia (1980). Similarly, Diaz and Hernandez (1980) and Romero and Castro (1983) studied *M. cephalus* in the San Andres lagoon in Tamaulipas and in the Mar Muerto in Chiapas, respectively. Yañez-Arancibia (1976) analyzed some aspects of feeding habits, growth, and maturity of *M. curema* in the coastal lagoon system of Guerrero. Comparative studies on *M. curema* and *M. cephalus* in Tamiahua lagoon, Veracruz, were carried out by the following authors: Perez-Garcia and Ibañez-Aguirre (1992) and Ibañez-Aguirre and Lleonart (1996) on relative growth

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Fish. Bull. 97:861–872 (1999).

and comparative morphometrics; Ibañez-Aguirre and Gallardo-Cabello (1996a) on total and natural mortality and Sanchez-Rueda et al. (1997) on the analysis of sediments in stomach contents. On the international scene, the studies on *M. cephalus* by de Silva (1980), Perera and de Silva (1978), de Silva and Silva (1979) in a coastal lagoon in Sri Lanka, Drake et al. (1984) in the coastal lagoon of San Fernando Cadiz, Cech and Wohlschlag (1975) along the coast of Texas, Broadhead (1958) along the coast of Florida, and Thompson (1963) in Australia, are worthy of mention, as well as those carried out by Alvarez (1976, 1979 and 1981), Richards and Castagna (1976), and Phillips et al. (1987) on *M. curema* .

In view of the above studies, the purpose of this study was to carry out an in-depth analysis of the growth characteristics of *M. cephalus* and *M. curema* with respect to length, sex, weight, and longevity in Tamiahua lagoon, Veracruz, Mexico.

Material and methods

Specimens were obtained from the commercial catch landed near Tamiahua lagoon, Veracruz, Mexico (Fig. 1). The most commonly employed fishing nets were gill nets of 35-mm mesh size (knot-to-knot) for *M. cephalus* and 30-mm mesh size (knot-to-knot) for *M. curema* . Sampling was carried out monthly during the first 8 days of each month for a year, from April 1991 to March 1992.

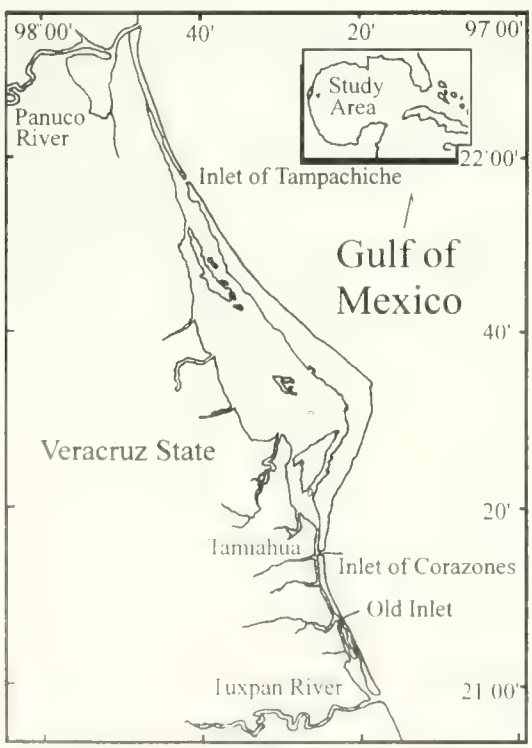

Figure 1
Map of the Tamiahua Lagoon, Veracruz, Mexico.

Total length (TL) was recorded from 2628 specimens of *M. cephalus* and 3354 of *M. curema* . For the study of growth, two independent readers examined scales, and otoliths (right sagitta) from 232 specimens of *M. cephalus* (122 females and 110 males) ranging from 200 to 400 mm and 292 specimens of *M. curema* (148 females and 144 males) ranging from 180 to 330 mm. The scales were cleaned, placed between two glass slides, and observed with transmitted light. The otoliths were submerged in a petri plate in xylol as a clarifying liquid and observed through a stereoscopic microscope with transmitted light. The analysis of the annual frequency variation of the fast growth rings (opaque) and slow growth rings (hyaline) of the margin of the otoliths showed that each year, one fast growth band and one slow growth band are deposited in the otoliths of boths species of mullets (Ibañez-Aguirre and Gallardo-Cabello, 1996b). It was reported earlier that otoliths give better results than do scales for the age determination of both species and make possible a definition of five age groups for *M. cephalus* and six for *M. curema* (Ibañez-Aguirre and Gallardo-Cabello, 1996b). These average lengths were used to obtain the constants for the von Bertalanffy equation (Table 1).

Ages "0" and "1" were not collected for *M. cephalus*, as a result of the mesh size of the nets; instead they were obtained by using the back-calculation method of Lea (1910, in Francis, 1990) and Bagenal and Tesch (1978, in Francis, 1990).

The constants for the von Bertalanffy equation (1938), L_∞, k, and t_0, were obtained by using the combined method of Ford (1933) and Walford (1946), and the methods of Gulland (1964), Tomlinson and Abramson (1961), Allen (1966), Beverton[1], Prager (1987), and Bayley (1977). Growth was also measured for each sex of both species. Growth curves for both species were obtained from the constants of the equation calculated by the above mentioned methods. The sum of the squared differences ($\sum e_i^2$) was used to compare the differences between calculated and observed values.

Hotelling's T^2 test (Bernard, 1981) was used to compare growth curves of the two sexes of both species. This test assumes that estimations of L_∞, k, and t_0 for both groups were obtained from two normal

[1] Beverton, R. J. H. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish Wildl. Serv., Fisheries Laboratory, Beaufort, Misc. Contrib. Rep., 181 p.

Table 1

Mean length (mm) employed for obtaining the growth parameters.

	Mugil cephalus					*Mugil curema*				
Age	Females (±SD)	Males (±SD)	Species (±SD)	*n*	Calculated values (±SD)	Females (±SD)	Males (±SD)	Species (±SD)	*n*	Calculated values (±SD)
"0"	156[1](± 9)	160[1](± 13)	158[a] (± 11)	0	158.34 (± 9)	187 (± 10)	176 (± 11)	183 (± 4)	4	184.20 (±9)
"1"	203[1](± 7)	207[1] (± 9)	204[a](± 7)	0	204.09 (± 9)	224 (± 8)	221 (± 9)	223 (± 7)	60	220.56 (± 11)
"2"	246 (± 5)	247 (± 19)	246 (± 14)	45	245.53 (±13)	251 (± 6)	250 (± 8)	252 (± 9)	71	252.15 (± 6)
"3"	283 (± 3)	281 (± 10)	282 (± 11)	59	283.04 (± 11)	276 (± 7)	276 (± 7)	278 (± 8)	66	279.60 (± 4)
"4"	319 (± 7)	315 (± 10)	317 (± 9)	44	317.01 (±11)	299 (± 6)	300 (± 4)	303 (± 7)	54	303.44 (± 3)
"5"	350 (± 9)	344 (± 8)	349 (± 12)	51	347.77 (± 8)	320 (± 4)	321 (± 4)	325 (± 8)	37	324.16 (± 4)
"6"	377 (± 8)	369 (± 6)	375 (± 12)	33	375.62 (± 11)	—	—	—		

[1] Average lengths obtained by back calculation.

Table 2

Estimates of the constants of the von Bertalanffy equation for *M. cephalus*, according to the different methods used.

	Species				Females				Males			
Method	L_∞(mm)	k	t_0	SD[2]	L_∞(mm)	k	t_0	SD[2]	L_∞(mm)	k	t_0	SD[2]
Walford-Gulland	637.97	0.0998	–2.8838	4.049	627.54	0.1052	–2.7342	2.186	609.05	0.1028	–3.0651	3.339
Beverton regression	637.97	0.1000	–2.8723	3.827	627.54	0.1053	–2.7281	2.110	609.05	0.1029	–3.0575	3.237
Tomlinson and Abramson	640.64	0.0998	–2.8418	3.211	627.24	0.1054	–2.7280	2.115	604.93	0.1043	–3.0376	3.341
Beverton regression	640.64	0.0998	–2.8400	3.211	627.24	0.1059	–2.6958	1.793	604.93	0.1050	–2.9860	2.725
Allen	642.00	0.0993	–2.8483	3.421	622.87	0.1074	–2.6709	1.794	603.52	0.1054	–2.9772	2.919
Beverton regression	642.00	0.0994	–2.8476	3.210	622.87	0.1074	–2.6697	1.783	603.52	0.1055	–2.9765	2.723
Prager	642.40	0.0993	–2.8480	3.210	622.90	0.1074	–2.6690	1.790	603.90	0.1054	–2.9770	2.722
Beverton regression	642.40	0.0993	–2.8499	3.209[1]	622.90	0.1074	–2.6699	1.782[1]	603.90	0.1054	–2.9791	2.722[1]
Bayley	640.00	0.1003	–2.8210	3.408	615.89	0.1094	–2.6620	2.382	608.34	0.1055	–2.8988	8.592

[1] The best fit.

distributions of joint probability, with three variables and one common variance.

The complete and eviscerated weights of 473 and 329 specimens of *M. cephalus* and *M. curema* , respectively, were recorded for the study of growth by weight. Weight data were recorded for each 20-mm length interval and the average weight for each size class was calculated.

The function $W = aL^b$ was used to obtain the weight-length relationship. Data for growth by length and the weight-length relationship were used to obtain the weight for each age. Growth by weight was obtained by substituting L_t and L_∞ by W_t and W_∞, respectively, obtained from the weight-length relationship in the von Bertalanffy equation. Taylor's equation (1958, 1960) was used to calculate age limit or longevity (95% of L_∞).

Results

Growth in length

Mugil cephalus The values for L_∞ and k were very similar (Table 2). The method that provided the greatest differences was that of Ford (1933) and Walford (1946). This similarity was due to the obtention of these constants; the t_0 value determined by Gulland

(1964) was also employed. Gulland recommends using just the age groups that are best represented and thus avoids errors due to a low representation of some poorly sampled age groups. Some calculations were repeated and the following t_0 values were obtained for the 3–5 years age groups: –2.74 (females), –3.07 (males), –2.89 (both species, sexes combined); and for the 3–6 age groups: –2.67 (females), –2.98 (males), –2.85 (both species, sexes combined).

The best fit was found with the t_0 result calculated for 3–6 years age groups. Thus, these values were used to obtain the average t_0 (Table 2). Use of the Beverton[1] equation improved the calculated values in comparison with the values observed by Ford (1933) Walford (1946), Tomlinson and Abramson (1961), Allen (1966), Bayley (1977), and Prager (1987) methods.

The calculated curve that best fitted values observed through otoliths corresponded to the parameters that were calculated with the Prager (1987) method and fitted with the Beverton[1] equation (Table 2). The calculated values of the lengths for different ages as well as their standard deviation (SD) were obtained by using these parameters for the two species (Table 1) which are consistent and, in general, show improved calculated values. Figure 2 presents the theoretical growth curve for *M. cephalus* ages 0–6 years.

During the first two years of life, striped mullet grew rapidly in length, with average increases of 45.8 mm during the first year and 41.4 mm during the second. From the third year on, growth decreased to annual increases in total length of 37.5 mm. Increases between the third and fifth years varied from 34.0 to 30.8 mm. Between the fifth and sixth years the increase was even smaller, with an average increase of 27.8 mm. In general, growth was high during the first two years of life and then decreased. This decrease is probably related to the time of first sexual maturity, which for this species occurs from 280 to 299 mm TL (males and females, respectively), which corresponds to an age of 3 years in both cases (Ibañez-Aguirre and Gallardo-Cabello, 1996b). L_∞ and k have a negative correlation, whereas L_∞ is high, the growth rate is low (Table 2).

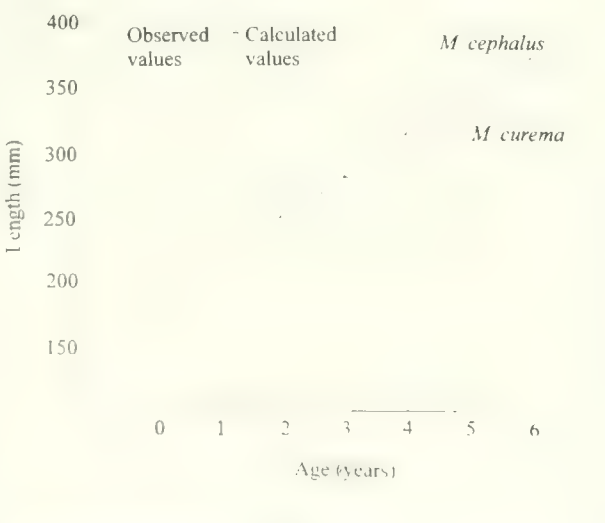

Figure 2

Theoretical growth curve for *M. cephalus* and *M. curema*

Mugil curema As can be seen in Table 3, L_∞ and k values obtained with the Ford (1933) and Walford (1946) method show the greatest difference with respect to the values calculated by the Tomlinson and Abramson (1961), Allen (1966), Prager (1987), Beverton,[1] and Bayley (1977) methods.

As with *M. cephalus* , new calculations for the t_0 value were made by using the Gulland (1964) method for the 1–4, 3–5, and 2–4 years age groups; the following t_0 values were obtained: for the 1–4 years age groups –3.94 (females), –3.03 (males), –3.62 (both species, sexes combined), for the 3–5 years age groups: –3.73 (females), –2.77 (males), –3.41 (both species, sexes combined) and for the 2–4 years age groups –3.72 (females), –2.75 (males), –3.39 (both species, sexes combined).

The von Bertalanffy curves showed the best fit for the calculated values of the 1–4 yr age groups. These values were used to obtain average t_0. The Beverton[1] equation with the above methods improved calculated values only in the case of the Ford (1933) and Walford (1946) method. The calculated curve that best fitted observed values through otoliths corresponded to the parameters calculated with the Prager (1987) method, as can be seen in Table 3.

Using these parameters, we calculated values for lengths at different ages, as well as their SD, which, as in the case of *M. cephalus,* are consistent and, in general, show improved calculated values (Table 1). Figure 2 presents the theoretical curve for growth in length of *M. curema* , for the ages of 0–5 years.

A high increase in length was recorded during the first year, after which growth decreased markedly. Size increased by 27.5 mm TL between the second and third years, 23.8 mm between the third and fourth years, and 20.7 mm between the fourth and fifth years. The decrease in growth from the first year on is related to the first sexual maturity, which in this species occurs in small sizes from 181 to 208 mm TL for males and females, respectively, at ages "0" and "1" (Ibañez-Aguirre and Gallardo-Cabello, 1996b).

Table 3

Estimates of the constants of the von Bertalanffy equation for *M. curema*, according to the different methods employed.

	Species				Females				Males			
Method	L_∞ (mm)	k	t_0	SD^2	L_∞ (mm)	k	t_0	SD^2	L_∞ (mm)	k	t_0	SD^2
Walford-Gulland	450.35	0.1511	−3.4372	14.921	444.98	0.1446	−3.7568	11.144	402.75	0.2026	−2.8121	30.593
Beverton regression	450.35	0.1494	−3.5039	11.547	444.98	0.1430	−3.8259	8.479	402.75	0.2000	−2.8816	23.712
Tomlinson and Abramson	458.44	0.1427	−3.5976	10.895	454.13	0.1358	−3.9352	8.041	411.99	0.1863	−3.0272	21.688
Beverton regression	458.44	0.1430	−3.5875	10.944	454.13	0.1360	−3.9283	8.057	411.99	0.1869	−3.0116	21.825
Allen	461.37	0.1406	−3.6238	10.866	454.58	0.1354	−3.9413	8.054	411.85	0.1865	−3.0256	21.688
Beverton regression	461.37	0.1408	−3.6167	10.885	454.58	0.1356	−3.9332	8.053	411.85	0.1871	−3.0097	21.830
Prager	461.40	0.1406	−3.6240	10.864[1]	454.60	0.1355	−3.9400	8.040[a]	411.80	0.1865	−3.0260	21.682[1]
Beverton regression	461.40	0.1408	−3.6170	10.885	454.60	0.1356	−3.9334	8.053	411.80	0.1872	−3.0090	21.833
Bayley	455.79	0.1451	−3.5559	11.134	449.60	0.1390	−3.8953	8.127	406.54	0.1931	−2.9721	22.057

[1] The best fit.

Growth between sexes

For *M. cephalus*, the growth curves that best fitted observed data were obtained with the Prager method (1987) and Beverton[1] equation (Table 2). In *M. cephalus* females the value of L_∞ is higher than in males, though the differencies between k values are small.

In *M. curema* the growth curves that best fitted observed values were obtained with the Prager (1987) method, as shown in Table 3. The k value in *M. curema* males is higher than in females; therefore males will reach L_∞ faster than females and the growth curve will be slightly more convex. Conversely, the females, showed a slighter growth curve and therefore greater longevity. However, in the case of *M. cephalus*, the k value was observed to be the opposite of that of *M. curema* .

Table 4 contains the values of the parameters and their variances calculated with the Prager method (1987) for both species. The results from the multivariate analysis show that females and males of *M. cephalus* and *M. curema* grow differently (Table 5). The calculated value of T^2 (8928.135) is considerably higher than the tabulated value (11.796, $P<0.01$) for *M. cephalus* and the same happens for *M. curema* , with a calculated T^2 (1843.808) and tabulated value (11.777, $P<0.01$).

Growth in weight

Length-weight relationship The relationships between length and weight stretch to be isometrical (Figs. 3 and 4). In length-weight relationships, dispersion is higher in *M. cephalus* because of the weight of gonads and viscera.

Theoretical growth in weight The theoretical weight for *M. cephalus* and *M. curema* in relation to each age group was obtained employing the mentioned weight equations (Figs. 5 and 6).

Longevity (Age $A_{0.95}$) Both species reach the 95% of L_∞ at the following ages:

Mugil cephalus	*Mugil curema*
$A_{0.95}$ = 28.32 years	$A_{0.95}$ = 18.68 years

The 95% of L_∞ is reached between sexes as follows:

Mugil cephalus	*Mugil curema*
Females = 26.24 years	Females = 19.17 years
Males = 26.46 years	Males = 14.04 years

Discussion

The parameters of the von Bertalanffy growth equation for *M. cephalus* in different areas of the Gulf of Mexico are shown in the Table 6. In the present paper, the value of k, calculated for *M. cephalus* is smaller than values presented by Marquez (1974) and Diaz and Hernandez (1980). Similarly, the values of L_∞ given from these authors are smaller than those obtained in our paper. On the other hand, differences of the growth parameters for the Texas coast (Cech and Wohlschlag, 1975) and Florida (Broadhead, 1958) are very pronounced in relationship to those obtained in our paper: the L_∞ values are smaller.

Table 4

Results of fitting the von Bertalanffy growth equation of females and males of *M. cephalus* and *M. curema*. Entries include parameters estimated and their estimated variance-covariance matrices (S).

Mugil cephalus

Males			Females		
L_∞ = 603.9	k = 0.10536	t_0 = −2.979	L_∞ = 622.9	k = 0.10736	t_0 = −2.669

	L_∞	k	t_0		L_∞	k	t_0	
L_∞	3.1701E+02	−1.1927E−01	−1.3055E+00		1.8417E+02	−0.5475E−01	−0.5870E+00	
k		0.4533E−04	0.5111E−03	$= S_m$		0.1642E−04	0.1810E−03	$= S_f$
t_0			0.6360E−02				0.2221E−02	

Mugil curema

Males			Females		
L_∞ = 411.8	k = 0.1865	t_0 = −3.026	L_∞ = 454.6	k = 0.1355	t_0 = −3.94

	L_∞	k	t_0		L_∞	k	t_0	
L_∞	6.8027E+02	−0.8253E+00	−7.3708E+00		8.7866E+02	−0.6123E+00	−8.3666E+00	
k		1.0212E−03	0.9428E−02	$= S_m$		0.4310E−03	0.6013E−02	$= S_f$
t_0			0.9296E−01				0.8794E−01	

Table 5

Results of the multivariate test between measured growth of males and females from *M. cephalus* and *M. curema*. Entries include the variance–covariance matrix (S) and its inverse (/S), the calculated T^2 statistic, the tabular F and T^2 statistics.

Mugil cephalus

249.7833	−0.08662	−0.94189	0.29749	1074.014	−20.9378
	0.000031	0.000344 $= S$		4216597	−102946 $= /S$
		0.004265			3914.545

$[-50 \quad 0.0097 \quad 0.12] = [P_m - P_f]'$

$T^2 = 8928.135^{**}$ $T^2_{0.01,\,3,\,245} = 11.79551$ $F_{0.01,\,3,\,245} = 3.9$

Mugil curema

795.2974	−0.7018	−7.94817	0.010014	−1.37597	0.99771
	0.000293	0.007448 $= S$		−2904.87	118.8114 $= /S$
		0.090049			89.34055

$[-42.8 \quad 0.052 \quad 0.914] = [P_m - P_f]'$

$T^2 = 1843.808^{**}$ $T^2_{0.01,\,3,\,405} = 11.77672$ $F_{0.01,\,3,\,405} = 3.9$

The values of the parameters of the von Bertalanffy growth equation for *M. cephalus* in different areas are also shown in Table 6. The values of k are higher for the coastal lagoons, whereas the L_∞ values are lower in relation to those obtained for the marine areas; all these differences are important even in areas that are very close (Kesteven, 1942; Thomson, 1951, 1963). Thomson (1951) and Broadhead (1953) found important variations in *M. cephalus* populations in adjacent estuaries; these differences can be explained because of the populational density and abundance of food. On the other hand, Oren (1981) showed that mugilids, because of the accessibility of the lagoons to the sea, can emigrate to the sea at least once per year and mix with other nearby populations. This exodus decreases the amount of local variation in local growth rates.

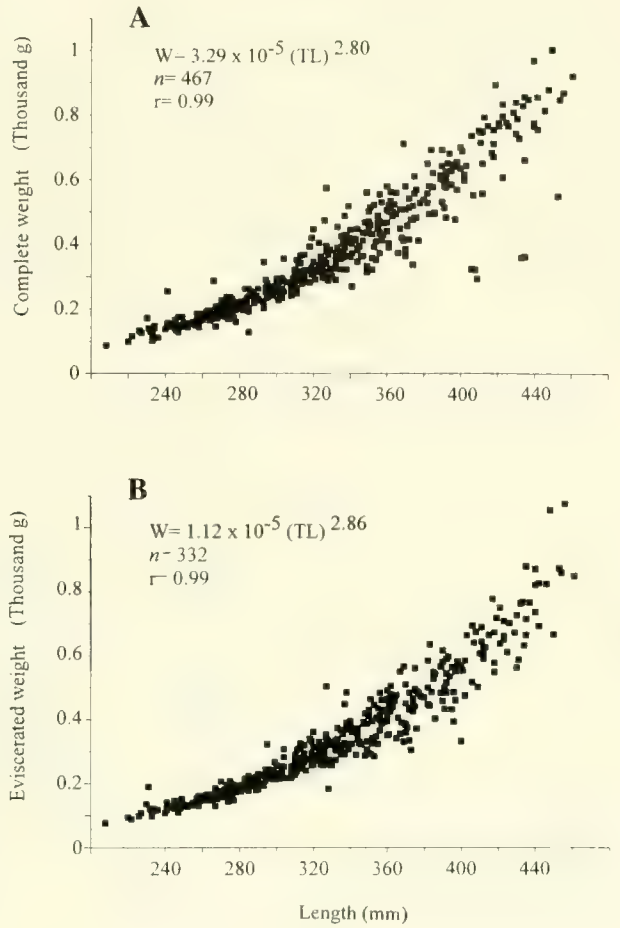

Figure 3

Relation between weight and length of *M. cephalus*: (**A**) complete weight; (**B**) eviscerated weight.

Finally, it is important to take into account that differences between growth rates are important even in areas that are very close; these differences could be explained by the different methods applied for age determination (Oren, 1981); however, these differences could be also explained by the world-wide distribution of this species and its different survival strategies. On the other hand, the differences between growth rates can also occur because of commercial exploitation, for when fishing is very intense, the commercial size of fish decreases and the variations of the k coefficient increase.

The values of the parameters of the von Bertalanffy growth equation for *M. curema* in different areas are shown in Table 7. In our paper, the value of k calculated for *M. curema* shows a higher position in relation to the value proposed by Alvarez (1979) and the value of L_∞ is higher in Cuba. On the other hand, the values of k obtained by Richards and Castagna (1976) in Virginia and by Phillips et al. (1987) in the Nicoya Gulf of Costa Rica show a higher position in relation to the k value obtained in our paper.

For the relation of growth between sexes, some authors have shown that there are no differences between sexes: for *M. cephalus*, Dannevig (1902); Kesteven (1942); Thomson (1951); Morovic (1957); Erman (1959); Thakur (1967); Cech and Wohlschlage (1975); Grant and Spain (1975); for *M. curema*, Alvarez (1979) and Angell (1973). On the other hand, Ezzat (1965), Brulhet (1974; 1975), and Farrugio (1975) have stated that there are differences in the growth between sexes. However, these latter authors did not infer whether these differences in the growth between sexes are significant or not from a statistical point of view. For this reason, a statistical test to compare the growth curves between sexes was

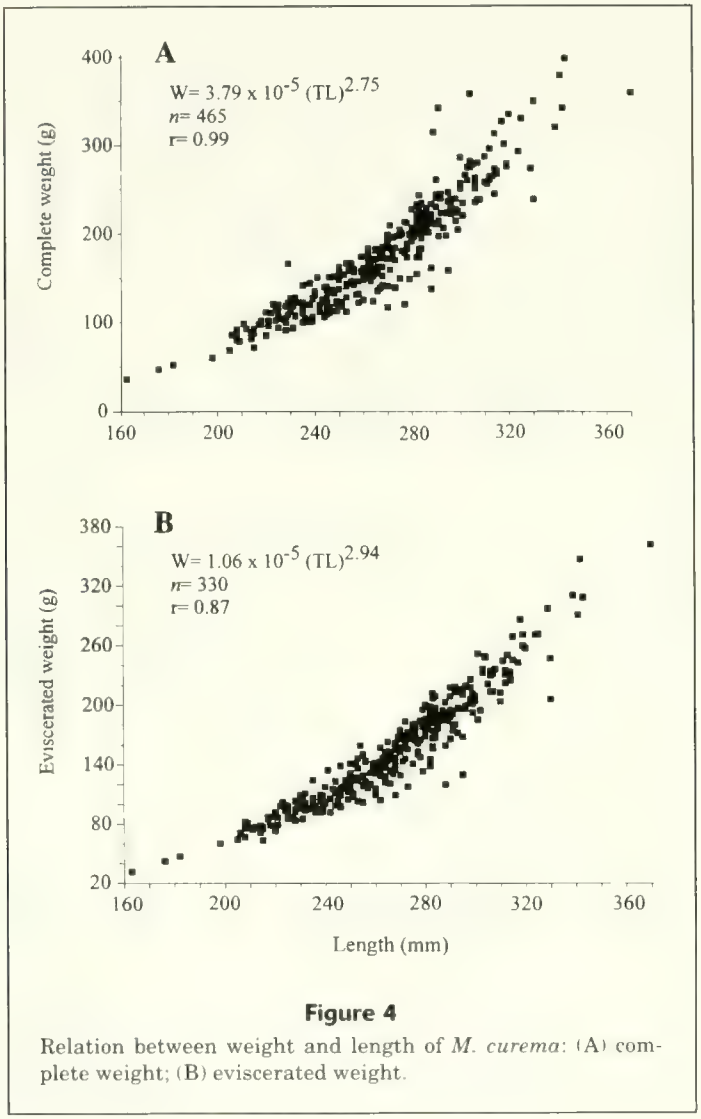

Figure 4

Relation between weight and length of *M. curema*: (A) complete weight; (B) eviscerated weight.

applied in our study (Tables 4 and 5); the results show that there are significant differences in growth between males and females for *M. cephalus* and *M. curema* . Oren (1981) mentioned: "sometimes the females grow slightly faster (Thomson, 1951; Hickling, 1970); Cech and Wohlschlag, 1975), live longer than the males (Thomson, 1951) or at least are predominant among older fish (Hickling, 1970)."

In general, the values of the relationship between length and weight obtained in our study are very similar to those expressed by other authors for coastal lagoons and marine areas. The results obtained for *M. cephalus* are similar to those shown by Kesteven (1942), Morovic (1954), Marquez (1974), Serbetis (1939), and Ezzat (1965). In the same way, the results obtained for *M. curema* are similar to those shown by Angell (1973) and Richards and Castagna (1976).

The longevity values for *M. cephalus* in different localities are given in Table 6. The highest values, 57.6 and 49.9 years, were found in the marine zones by Ilin (1949) in the Black Sea and Kesteven (1942) in Australia, respectively. The lowest values were obtained by Broadhead (1958), 3.7 for males and 4.5 years for females of this species in the marine zones, and by Heldt (1948), 4.6 years in coastal lagoons.

The values of longevity for *M. curema* in different areas are shown in the Table 7. The highest value was obtained by Alvarez (1979), 30 years in Cuba, and the lowest by Richards and Castagna (1976), 3.8 years in Virginia.

The longevity values obtained in the study, 28.3 and 18.7 years for *M. cephalus* and *M. curema,* respectively, showed an intermediate position in relation to the values found by other authors. In all cases, as Taylor (1958) has shown, the longevity and

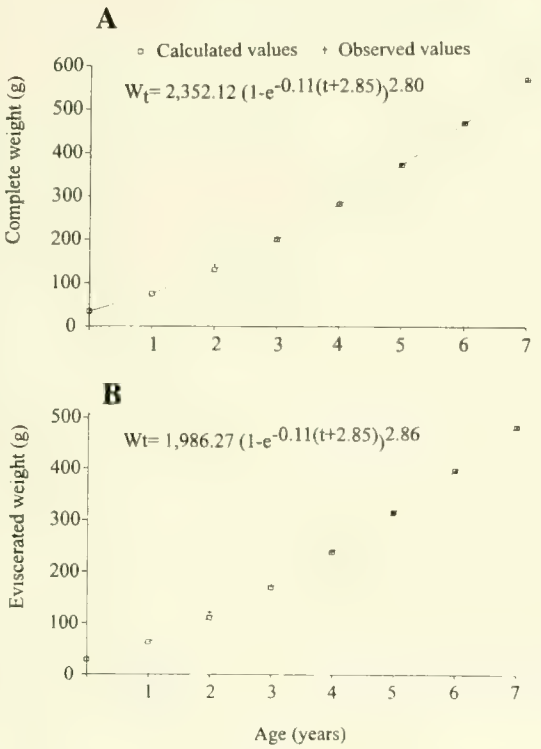

Figure 5

Theoretical growth curve of *M. cephalus*: (A) complete weight; (B) eviscerated weight.

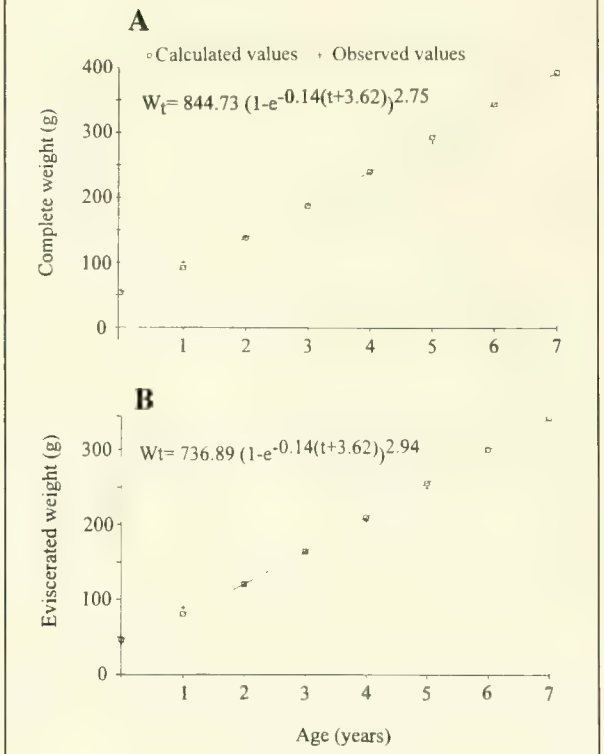

Figure 6

Theoretical growth curve of *M. curema*: (A) complete weight; (B) eviscerated weight.

Table 6

Growth parameters of *M. cephalus* for the Gulf of Mexico and other localities. TL = total length, F = female, M = males, Sp. = species. This table was modified from Tables 5.4 and 5.5 in Oren (1981).

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}{}^1$
Gulf of Mexico								
Coastal lagoons								
This study	Tamiahua, Mexico	Otoliths	TL	F	622.9	0.11	–2.670	26.2
		Otoliths	TL	M	603.9	0.11	–2.979	26.5
		Otoliths	TL	Sp.	642.4	0.10	–2.850	28.3
Marquez, 1974	Tamiahua, Mexico	Scales	TL	Sp.	510.0	0.34	–0.114	8.8
Diaz and Hernandez, 1980	Tamaulipas, Mexico	Scales	TL	Sp.	588.0	0.19	–0.213	15.4
Marine zones								
Cech and Wohlschlag, 1975	Texas, USA	Scales	TL	F	407.0	0.32	–0.710	9.4
		Scales	TL	Sp.	450.0	0.24	–0.900	12.5
Broadhead, 1958	N & NW Florida USA	Scales and tag	TL	F	374.0	0.82	–0.160	3.7
		Scales and tag	TL	M	379.0	0.66	–0.036	4.5
Other localities								
Marine zones								
Ilin, 1949	Black Sea	Scales	TL	Sp.	1089.0	0.05	–1.620	57.6
Kesteven, 1942	Australia	Scales	TL	Sp.	1729.0	0.06	–0.510	49.9
Thompson, 1951	West Australia	Scales	TL	Sp.	609.0	0.30	–0.143	10.0
Thompson, 1963	Australia	Scales	TL	Sp.	727.0	0.23	0.006	13.1

continued

Table 6 (continued)

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}$[1]
Coastal lagoons								
Romero and Castro, 1983	Chiapas, Mexico	Scales	TL[2]	Sp.	458.5	0.21	–1.770	14.4
Ezzat, 1964	France	Otoliths	TL	Sp.	417.7	0.47	–0.169	6.4
Serbetis, 1939	Rome, Italy	Scales	TL	Sp.	563.0	0.56	0.083	5.3
Morovic, 1954	Venice, Italy	Scales	TL	Sp.	611.0	0.21	–0.465	14.3
Alessio, 1976	Orbetello, Italy	Scales	TL	Sp.	615.0	0.40	–0.044	7.5
Morovic, 1957	Vransko, Yugoslavia	Scales	TL	Sp.	590.0	0.23	–0.083	12.8
Heldt, 1948	Tunisia	Scales	TL	Sp.	620.4	0.65	–0.048	4.6
Farrugio, 1975	Tunisia	Scales	TL	Sp.	693.0	0.19	–0.630	15.8

[1] These values of longevity were obtained in our study by the application of the Taylor method (1958) to the growth parameters given by the authors mentioned in this table.
[2] For the conversion from standard length to TL, the equation given by Thompson et al. (1991) was used

Table 7

Growth parameters of *M. curema* for other localities.

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}$[1]
This study	Tamiahua, Mexico	Otoliths	TL	F	454.6	0.14	–3.900	19.2
		Otoliths	TL	M	411.8	0.19	–3.000	14.0
		Otoliths	TL	Sp.	461.4	0.14	–3.600	18.7
Richards and Castagna, 1976	Virginia, USA	[2]	TL[3]	Sp.	403.4	0.78	–0.060	3.8
Alvarez, 1979	La Habana, Cuba	Spine	TL	Sp.	532.0	0.10	–5.900	30.0
Phillips et al., 1987	Costa Rica	[2]	TL	Sp.	432.0	0.60	–0.244	5.0

[1] These values of longevity were obtained in our study by the application of the Taylor method (1958) to the growth parameters given by the authors mentioned in this table.
[2] = method not indicated.
[3] For the conversion from fork length to TL, the equation given by Thompson et al. (1991) was used.

L_∞ show an inversely proportional relation to the k coefficient.

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Direct observations on the hooking behavior of Pacific halibut, *Hippoglossus stenolepis*

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Abstract.—Direct observation of a 6-hook model setline off Canada's northwest coast with an underwater camera allowed estimation of approach direction, attack rate, and hooking success for Pacific halibut (*Hippoglossus stenolepis*). In observations of 129 halibut approaches, 29 halibut simply continued swimming past the gear and away. The remaining 100 halibut responded in some way to the gear, exhibiting behaviors ranging from a simple change in swimming direction toward the gear, to bites on the baited hooks. Behavior transitions are described both leading up to and following 57 observed bites. Halibut displayed a positive rheotactic response; 74% approached upstream toward the bait. A higher proportion of upstream approaches resulted in bites than approaches from other directions or approaches that occurred during slack current. Most bites were associated with a vigorous rushing behavior, which often led to hooking. Hooking success was demonstrated to be length-dependent, ranging from zero for the smallest fish to approaching one for the largest sizes caught. Very low rates of hooking success were observed for some rockfish, which in some areas are important bycatch species of the halibut fishery.

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The International Pacific Halibut Commission (IPHC) sets harvest quotas for the stock of Pacific halibut (*Hippoglossus stenolepis*) off the Pacific shores of the United States and Canada. An important tool in setting these quotas is the catch per unit of effort (CPUE) both of the directed commercial fisheries of these countries and of setline surveys conducted annually by the IPHC. The trends in these CPUE indexes, both among areas and over years, are important to the IPHC stock-assessment model. Over the years, the IPHC has conducted fishing experiments in order to understand different aspects of CPUE. A selection curve for the size 16/0 J-style hooks used in the fishery prior to 1984, demonstrated by Myhre (1969), ranged from zero for fish around 40 cm, to one for fish around 80 cm. The mechanism for size selection in halibut has not been demonstrated. Skud (1978) reported that halibut was a dominant predator, probably more successful than other species in competing for setline baits, and concluded that although other fish and invertebrates, even if not caught, could cause bait loss, competition by these species was unlikely to affect the CPUE of halibut. Later studies with circle hooks (Hoag et al., 1984; Kaimmer and St-Pierre, 1993) demonstrated effective competition by a decreased catchability of halibut associated with the presence of large numbers of spiny dogfish (*Squalus acanthias*).

Attack rate (bites/fish) and hooking success (hookings/bite) by fish length are important parameters of most hook-catch models (Deriso and Parma, 1987), although these parameters often must be estimated from either a theoretical model or observations of captive fish. This paper presents results from an IPHC study designed to estimate these parameters directly from observations of halibut approaches and of bites on the circle hooks used in the present-day fishery. These behavioral studies conducted in the field, rather than through observation of captive fish, should yield results most applicable to and representative of setline catches of wild fish (Løkkeborg et al., 1993).

Materials and methods

Vessel and area

A 12-day experiment was conducted 11–20 June 1994 from a 15.5-m chartered vessel. An underwater camera permitted a view of a model setline consisting of six baited fishing hooks. The gear was placed at various halibut habitats in the Queen Charlotte Islands of British Columbia, Canada. This region was chosen to provide an opportunity to view a variety of halibut habitats, in terms of depth and bottom type, with a likelihood of relatively good water clarity. The midsummer timing allowed for the presence of halibut on their midyear feeding grounds, long working days, the opportunity of fair weather, and a window between expected plankton

blooms. Camera equipment was deployed 45 times, primarily off the northern and northwestern shores of the Queen Charlotte Islands (Fig. 1). Bottom habitat ranged from mud or soft sediment, gravel, cobbles, or large boulders, to steep ledges. Deployments were intended to last about one hour. Problems with strong currents or the loss of four or more baits due to fish captures or other reasons resulted in early gear retrievals. Longer deployments resulted from gear retrieval problems. Time on bottom for each deployment averaged 58 min (range 14–150 min, SD 28 min). Average depth for all sets was 67 m (range 11–84 m).

Equipment

A silicone-intensified tube (SIT) monochrome video camera (model OE1323, Osprey Electronics Ltd., Aberdeen, Scotland) was housed in an enclosure featuring both pan and tilt functions. This enclosure was mounted in an aluminum cage connected by 5-cm aluminum pipe to a square base frame constructed of 5-cm steel pipe (Fig. 2). The camera–frame assembly was deployed by, and monitored through, an electromechanical cable. All observations were made by using ambient available light.

A 0.8-cm (5/16-inch) diameter groundline was suspended about 30 cm inside the base frame by short lengths of elastic cord attached to the inside corners of the steel frame. This arrangement resulted in an elastic attachment for the hooks and gangions. This "soft" attachment was probably a more realistic model of the behavior of a gangion on a groundline than an attachment made directly to the rigid steel frame. The study used 16/0 circle hooks (O. Mustad and Sons, Oslo, Norway, Quality 39965), the size and style most commonly used in the Pacific halibut fishery, and the standard in IPHC surveys. Hooks were attached by 81-cm (32-inch) gangions and snaps to the suspended groundline, one per side alternating with two per adjacent side, for a total of six hooks. All hooks were baited with 0.17-kg (1/3-lb) pieces of chum salmon (*Oncorhynchus keta*) fillet with skin intact.

Observation of a 25-cm length of flexible surveyor's tape attached to one of the aluminum legs, as well as of dust or sediment plumes during bait attacks, was used to determine the direction of bottom current and also as a qualitative measure of current strength. The video signal was monitored and recorded at all times. When viewed directly from above, all parts of the square base were within the field of view. This usually meant that all six hooks could be viewed at the same time. When one or more hooks lay outside the base frame, the camera was periodically redirected for viewing these outside hooks.

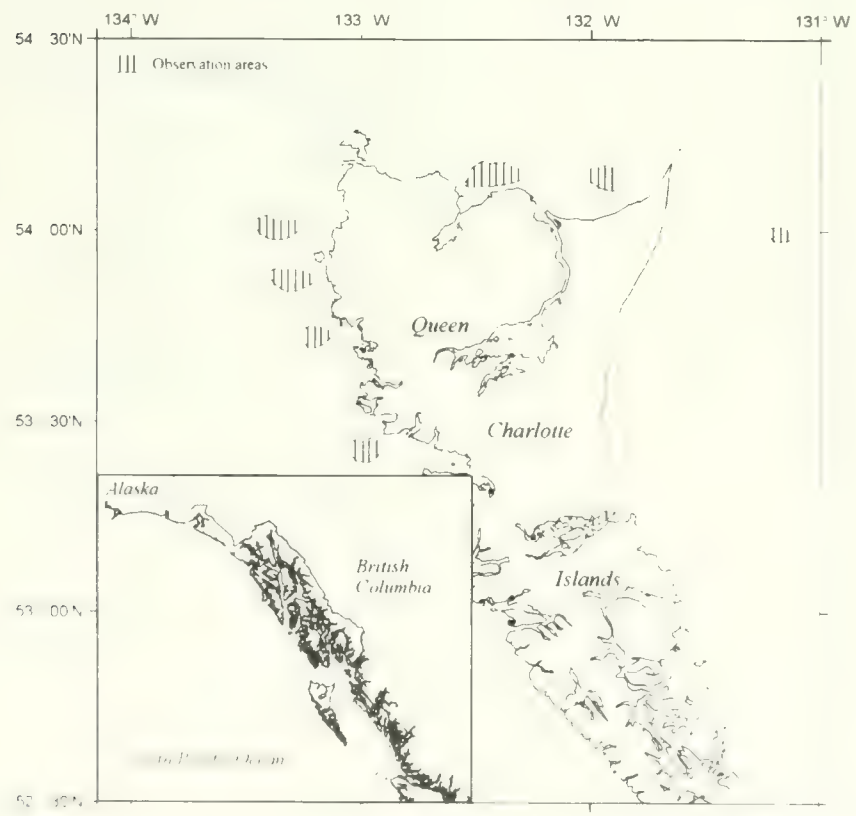

Figure 1

Location of camera deployments. Box in inset shows general area of operation.

Fish length and distance measurements

Lengths of 20 hooked and landed halibut were measured. During video editing, relative fork lengths for all halibut that could be clearly viewed on or near the bottom and at or near the center of the frame were obtained by using a vernier caliper held against the video screen while the video image was frozen. The linear regression between measured and relative fork length (r= 0.74) was used to estimate the fork lengths of 92 fish not captured and retrieved, as well as the distance from fish lying on the bottom to the nearest baited hooks. Caught fish, other than halibut, were weighed to the nearest 0.5 kg on a spring scale.

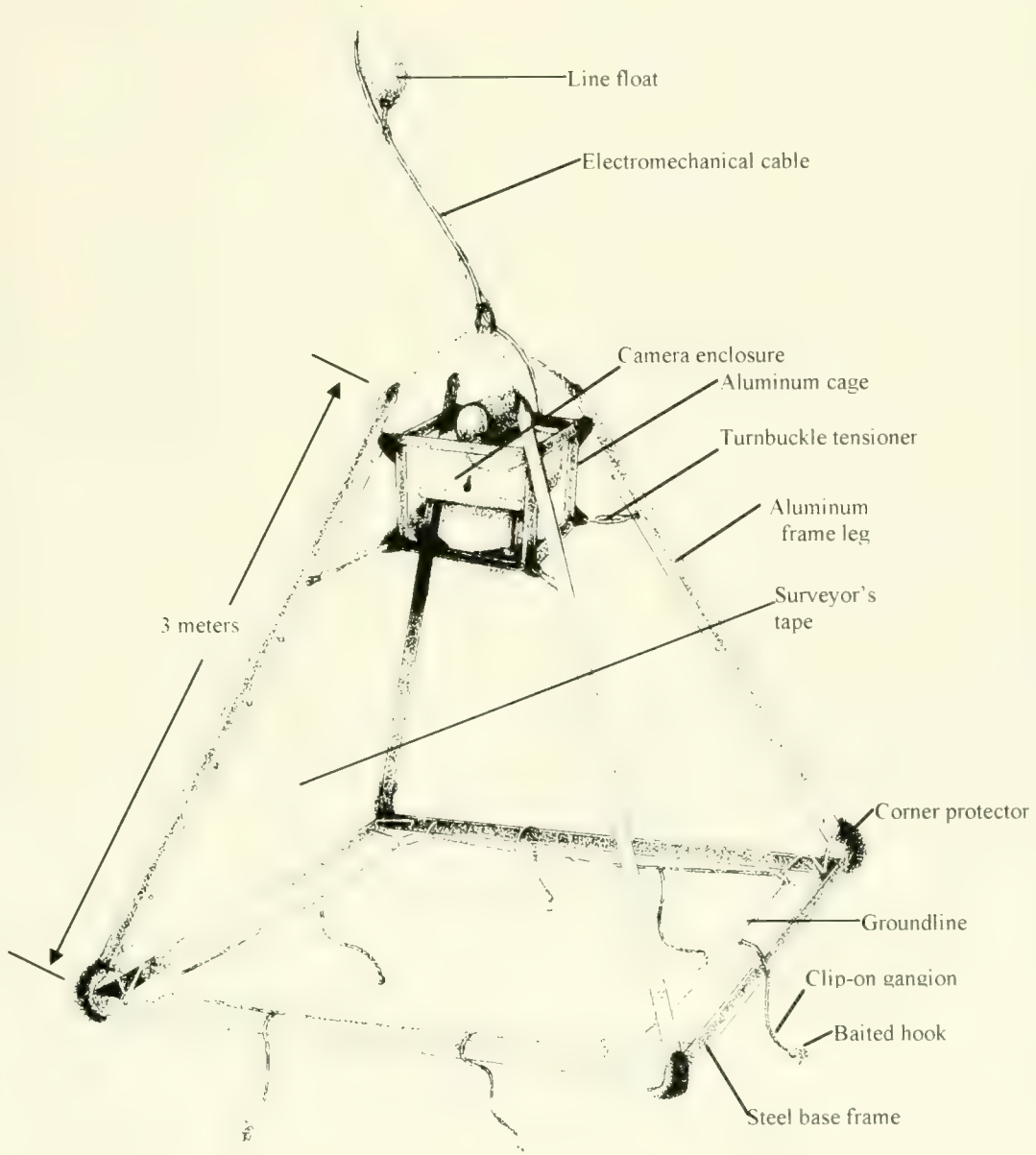

Figure 2
Camera cage and frame, showing attachment of groundline and baited hooks.

Observations of behavior

Appearance and subsequent behavior sequences were recorded for all halibut, including the directions of both appearance and departure in relation to the bottom current. All behaviors were coded as to time at which the behavior either occurred or was initiated, to the nearest second. Behavior codes were modified from those used by Fernö et al. (1986). For species other than halibut, only bites and hookings were recorded. Unless otherwise specified, code descriptions and frequencies refer to halibut only.

Behavior definitions

The word "observed" was recorded upon the first appearance of a halibut, along with its approach direction in relation to the bottom current, and a number was assigned to the fish in order to identify future observations on that fish.

The word "looping" was recorded when a swimming fish made a turn of more than 90 degrees.

"Lying" was recorded when a fish stopped swimming and lay on the bottom, and included (for fish that lay near hooks) direction to the closest baited hook in relation to bottom current.

"Biting" was recorded when a fish took a baited hook completely into its mouth.

An "incomplete biting" was recorded when a fish touched a bait but the bait or hook was never completely within its mouth.

"Grazing" was recorded if a fish bit at a piece of bait that was not attached to a hook. Pieces of bait would occasionally fall free from the hook during the rushing following a bite.

"Rushing" was recorded when a fish swam rapidly forward with the bait or hook in its mouth.

"Spitting" was recorded when bait was either spat or pulled out of a fish's mouth.

"Hooking" was recorded when a fish retained a hook in its mouth for at least twenty seconds, usually while the fish struggled or fought violently. This time period was chosen as consistent with that in other literature on hooking behavior (Fernö et al., 1986; Huse and Fernö, 1990). However, hooking was not recorded until completion of the rushing behavior. When biting was followed by rushing lasting more than twenty seconds, which was in turn followed by spitting, that portion of the behavior sequence was listed as "biting, rushing, spitting." A fish that rested after rushing with the hook still in its mouth, and which subsequently after twenty seconds or more rushed and spat out the hook, was listed as "biting, rushing, hooking, lying, rushing, spitting."

"Attacking" was recorded when a fish chased or bit at another fish, either a halibut or one of the other species in the viewing area.

"Departure" was recorded, along with direction of travel in relation to bottom current, when a fish left the observation area. Occasionally, a fish would leave the observation area and be identified on its subsequent return by a short duration of absence (less than 5 s), and by its length, and body markings. In these cases, the period of nonobservation was recorded as "looping."

Sequential occurrences of either lying or looping were coded as single occurrences. Consecutive lying behaviors were coded as a single behavior occurrence only when the subsequent lying was the result of a small position shift and the fish did not shift to a different bait. Twenty-one occurrences of behaviors were considered compromised by the experimental setup. A behavior transition beginning with a compromised behavior was considered invalid. For example, a bite where the hook or gangion was wrapped around the frame was considered compromised, and the transition to the following behavior was considered invalid.

Direction in relation to bottom current

Fish approaching or departing within 67.5° to either side of and into the current were coded as "upstream." Fish swimming within the next 45° on either side of the current (within a 22.5° arc to a line perpendicular to the current) were coded as "right angle to the current." Fish swimming within 67.5° to either side of and out from the current were coded as "downstream." These same criteria were used to record the direction in which a fish was lying in relation to a bait.

Results

The number of halibut observed was 129, ranging from none (on 19 sets) to a high of 19 (on one set). On average, 5.6 halibut were observed on sets where at least one halibut was seen, and the numbers of halibut caught per set ranged from 0 to 4. Measured fish ranged from 72 to 114 cm in length (mean=86.8 cm, SD=11.4 cm). Calculated lengths ranged from 52 to 196 cm (mean=90.1 cm, SD=24.2 cm).

Behaviors and behavioral transitions

The time until first appearance of the first halibut in a set varied widely, ranging from almost immediately (18 s) to more than an hour after the gear was set (1 h 1 min), and averaged 18 minutes (SD=13 min 32 s). For 29 fish that swam away immediately after observation, the time between appearance and departure ranged from 7 to 33 seconds (mean=9 s, SD=7 s). Orientation in relation to bottom current was noted for 93 halibut approaches (Fig. 3). Another 18 approaches were noted as occurring during slack current. Of those fish that approached during periods of noticeable current, 75% approached upstream, 9% approached at right angles to the current, and 17% approached downstream.

Looping and lying were the most common behaviors, with 80 loopings recorded for 60 halibut and 70 lyings recorded for 45 halibut (Table 1). The average durations of looping and lying behaviors were 40 and 14 seconds, respectively (Table 2). Fifty-seven bites were observed; 48 halibut made a single bite, 3 halibut made 2 bites, and 1 halibut made 3 bites. A total of 25 halibut were classed as hooked. The transition matrix in Table 3 details 426 valid behavior transitions constructed from the observations. The main

function of the matrix was to show possible patterns or combinations of behaviors that occurred more or less frequently than expected if all possible behavior transitions had the same probability of occurring. Statistical analysis of this matrix is complicated by the fact that not all transitions were possible (a spitting may only follow after biting or rushing). The matrix was therefore visually inspected for large differences, as recommended by Slater (1973).

Prebiting behavior and attack rate

There were 293 transitions observed for halibut, not including behaviors that followed initial complete bitings. The number of prebiting transitions per individual fish ranged from one to fifteen, with 78% of the fish making three or less transitions, and over 90% making five or less.

Looping and lying near bait were the most common behaviors following initial observation. Less commonly observed were departures, biting, and incomplete biting. Looping behavior was followed about equally by lying near bait, biting, and departure. Lying near bait was most often followed by either looping or biting, and less often by departure or an incomplete biting. For 71 occurrences of lying behavior, 8 either had no obvious hook orientation or occurred during slack current, 3 fish lay upstream of bait, 26 lay to the side of bait, and 34 lay downstream from bait. The distance from bait for fish lying beside or downcurrent averaged 13.2 cm (SD=8.4 cm) and 14.6 cm (SD=9.0 cm), respectively. Incomplete biting was most often followed by lying near bait, and less often by departing or looping.

The transitions in Table 3 do not consider preceding behaviors, or how many previous behaviors a particular fish had completed. As each of the original 129 halibut was observed through the first four behavior transitions up to either biting or departing, there was a tendency for fish to stay in interaction with baits. Lying, incomplete and complete biting, and grazing are all behaviors that are direct interactions with either the bait or food present around a baited hook. In the first transition (n=129), fish were most likely to interact with bait (43%), loop (34%), or depart (23%). About one-third of the bait interactions in the first transition were bites. In the second transition (n=78), fish were most likely to interact with the bait (57%) or depart (40%). Only 12% looped. Again, about one-third of the bait interactions were bites. By the third transition (n=28), fish were much more likely to continue bait interactions (68%) than they were to loop (25%) or depart (7%). About one-quarter of bait interactions were bitings.

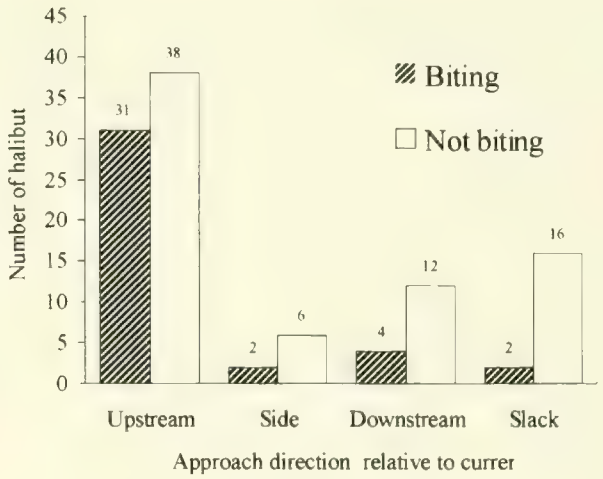

Figure 3

Numbers of halibut biting and not biting, by approach direction in relation to bottom current.

Table 1

Frequencies of halibut behaviors observed. Individual fish may be counted as performing more than one behavior.

Behavior	Count	Number of individual fish
Appearance	129	
Looping	80	60
Lying	70	45
Incomplete biting	15	9
Biting	57	52
Rushing	53	48
Hooking	25	25
Spitting	30	27
Grazing	4	3
Attacking	3	3
Departure	96	—
Grand total	562	

In the fourth transition (n=21), 62% continued with bait interactions, almost half of which were bitings, 21% departures, and 19% loopings. By the end of the fourth behavior transition, out of the original 129 halibut observed, approximately half (66 fish) had departed, whereas just over a third (47) had made complete bites. In each of the transition levels, 43–68% of behaviors were directed toward baits.

Elapsed time between appearance and the first observed bite for all halibut ranged from 1 s to 7 min 54 s (mean=34 s, SD=1 min 5 s). Ninety-five percent

of first bites occurred in less than 1 min 20 s after first appearance, and 50% occurred within the first 20 s. Although no significant difference was noted between time to first bite and approach direction, for the 36 observations where the approach was made during some current, the maximum time to first bite was 2 min 51 s. Of two bites following appearances during slack current, one bite occurred almost 8 min

Table 2

Duration of observed halibut behaviors.

Behavior	No. of observations	Duration	
		Range	Average (±SD)
Prior to hooking			
Looping	80	3 s–6 min 32 s	40 s (±62 s)
Lying (prior to hooking)	70	1–68 s	14 s (±15 s)
Rushing (followed by spitting)	31	1–63 s	10 s (±13 s)
Rushing (followed by hooking)	22	24 s–3 min 30 s	86 s (±44 s)
Following hooking			
Lying	34	3 s–22 min 8 s	3 min 49 s (±5 min 19 s)
Rushing	24	8–78 s	31 s (±19 s)

Table 3

Transition matrix of observed values (upper number) and expected values (in parentheses) for the frequency of transitions from one behavior to another within behavior sequences. Top row is the first behavior in a transition and the leftmost column is the second behavior. For example, a fish that was observed, made one loop, and then swam away would have two tallies in this table, one for "appearance" followed by "looping," and a second for "looping" followed by "departure." Behavior transitions starting with compromised behaviors are not included in this table.

	First behavior									
Second behavior	Appearance	Looping	Lying	Incomplete biting	Grazing	Biting	Rushing	Spitting	Attacking	Total
Departure	29 (38.0)	30 (28.7)	12 (25.3)	3 (3.8)	— (0.9)	—	—	20 (8.8)	— (0.6)	94
Looping	44 (31.1)	—	21 (20.7)	2 (3.1)	— (0.7)	—	—	9 (7.2)	1 (0.5)	77
Lying	32 (28.3)	27 (21.4)	—	8 (2.8)	2 (0.7)	—	—	— (6.6)	1 (0.4)	70
Incomplete biting	4 (6.1)	1 (4.6)	10 (4.0)	— (0.6)	— (0.1)	—	—	— (1.4)	— (0.1)	15
Grazing	— (1.6)	1 (1.2)	3 (1.1)	— (0.2)	— (0.0)	—	—	— (0.4)	— (0.0)	4
Biting	19 (23.1)	15 (17.4)	21 (15.3)	1 (2.3)	— (0.5)	—	—	1 (5.4)	(0.4)	57
Rushing	—	—	—	1 (2.1)	—	52 (27.2)	—	—	—	53
Spitting	—	—	—	—	—	2 (14.9)	27 (27.4)	—	—	29
Hooking	—	—	—	—	—	1 (12.9)	24 (23.6)	—	—	25
Attacking	1 (0.8)	— (0.6)	— (0.5)	— (0.1)	1 (0.0)	—	—	— (0.2)	— (0.0)	2
Total	129	74	67	15	3	55	51	30	2	426

after initial appearance, more than twice the longest elapsed time between appearance and first bite for fish that appeared when bottom current was noticeable.

There were differences in the biting behavior of halibut associated with their direction of approach in relation to bottom current (Fig. 3). The difference was significant (upstream 45%, side or downstream 25%; χ^2=33.1, P<0.0125), as was the difference between fish that approached when current was or was not noticeable (current 49%, no current 11%; χ^2=5.4, P<0.0125). Overall, attack rate (bites/fish) was 33–73% over the range of lengths observed (Table 4). Although approach direction in relation to current had a significant effect on attack rate, there was no relation between fish length and attack rate for 41 halibut that had approached upstream. For these fish, the attack rate for fish less than 82 cm (sublegal size) was 46% (11 of 24), and the rate for fish 82 cm or larger (legal size) was 47% (8 of 17).

Direction in relation to the current was noted for 54 departures. Thirty-three (61%) halibut departed upstream, 6 (11%) departed at right angles to the current, and 15 (26%) departed downstream.

Postbiting behavior and hooking success

Almost all bites (95%) occurred while fish were in motion: a fish swam toward the bait, took the bait in its mouth, and continued swimming (rushing). In two cases, a lying fish took bait and subsequently spat it out without rushing. In one case, a lying fish kept the bait in its mouth long enough (20 s) to be classified as hooked, but without rushing.

Rushing behavior was about equally followed in frequency by either spitting the hook (53%) or hooking (47%). On average, spitting occurred 10 s after the start of rushing behavior; rushing that did not result in spitting had an average duration of 86 s (Table 2). In two-thirds of the cases where the hook was spat, the fish departed rapidly. Thirty percent of spittings were followed by looping behavior and, in one case, the fish immediately rebit the hook. One "steal" was observed, where the fish swam free from the hook with the entire bait in its mouth. Hooking success (hookings/bite) by 5-cm length group was 0–83% and increased steadily with increasing fish size. The difference in hooking success between fish of sublegal (<82 cm) and legal (≥82 cm) length was highly significant (38% vs. 71%; χ^2=4.36, df=1, P<0.025).

Figure 4 shows observed postbiting behavior transitions, from an initial complete bite by an individual fish through the fourth behavioral transition. Of 50 fish tracked on this chart, 20 ended up departing, 22 ended up hooked, and 3 were still interacting with hooks at the end of the fourth behavioral transition. Of the three continuing interactions, one fish lay near bait and two fish rebit baited hooks. Fifty percent of

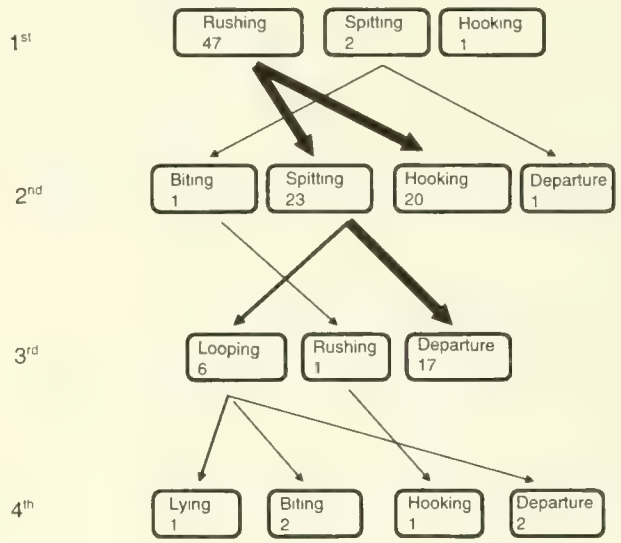

Figure 4

Behavior tree describing behavior sequences following an initial complete bite. Numbers at left of rows are the position of behaviors in sequences following initial observation. Numbers in boxes are the total frequencies of each behavior in a row position. Thickness of arrows represents relative numbers of observations for each behavior transition. Because some behaviors were compromised, not all behaviors have transitions from one row position to the next.

Table 4

Halibut attack rate (% of fish biting) and hooking success (% of bites resulting in hooked fish) by 5-cm group.

Size class (cm)	Number observed	Number of bites	% bites	Number hooked	% hooked
62–67	6	3	50	0	0
68–72	11	5	45	1	20
73–77	17	9[1]	53	3	38
78–82	11	8	73	5	63
83–87	12	5	42	3	60
88–92	18	6	33	4	67
93–97	12	6	50	5	83
Total	87	42		21	

[1] One bite in the 73–77 cm size class was compromised. Percentage hooked is determined from the eight uncompromised bites.

spits occurred in less than 5 seconds, and 95% occurred in less than 25 seconds. Once hooked, and after initial rushing, the halibut lay on the bottom, resting, then went into a pattern of rushing, resting, rushing, etc. There appeared to be a pattern of decreasing duration of rushing following subsequent rest periods. The average times for resting and rushing after the initial hooking were 3 min 49 s, and 31 s, respectively (Table 2).

Hooking success for other species

The range of approach and interaction behaviors for species other than halibut was not documented beyond noting bitings and subsequent hooking. Other species that bit at hooks included canary rockfish (*Sebastes pinniger*), yelloweye rockfish (*S. ruberrimus*), quillback rockfish (*S. maliger*), ratfish (*Hydrolagus colliei*), and lingcod (*Ophiodon elongatus*). In general, hooking success for the major rockfish species was around 5–6% (Table 5). These fish were comparable in average size (weight) to those caught as incidental catch in the directed halibut fishery.

Discussion

The feeding behavior of halibut may be classified into three phases: arousal, search, and bait attack and food ingestion.

Arousal

In most cases, arousal to the presence of food occurs at a distance, and bait odor carried by bottom currents attracts fish from well beyond the limited viewing distance of the present experiment. Although undoubtedly involving detection of an odor plume (Atema, 1980), the present experiment did not investigate the initial arousal phase of feeding behavior.

Table 5
Hooking success for species other than halibut.

Species	Number of bites	Number hooked	% hooked	Average weight (kg) of hooked fish
Canary rockfish	339	17	5	4.0
Yelloweye rockfish	237	20	8	3.8
Quillback rockfish	228	9	4	1.9
Ratfish	36	1	3	N/A
Lingcod	23	9	39	11.1

However, a number of observations in relation to food location and uptake were made.

Search

It is clear that halibut use orientation to bottom current to locate food, most approaching upstream when a bottom current was present. This rheotactic orientation is used by many fish for detection and location of prey (Atema, 1980; Løkkeborg et al., 1989; Løkkeborg, 1998). Once fish are aroused to the presence of a prey item by scent, they orient into a current to locate the food.

The role of vision in food location by Pacific halibut was less clear. Behaviors directed towards the gear were observed in some cases immediately after the gear reached the seafloor. These were likely responses to visual clues. However, the greatest number of appearances appeared to be motivated by scent carried by the current. Although earlier studies have shown that halibut certainly prey on a number of pelagic or semipelagic species where vision must play an important role in prey recognition and capture (Best and St-Pierre, 1986), it probably played a limited role in behavior toward the model setline.

Prebiting behavior and attack rate

Fish vary widely in their reliance on sight, smell, and touch in deciding whether to accept or reject food once it has been located (Løkkeborg, 1994). Both looping and lying behaviors were common in the observed halibut, and in only a few cases was a complete bite initiated without some preliminary bait interaction such as looping or lying. Looping behavior could be a test of an odor plume by the fish, assuring that the fish is in an area of high-scent concentration. Many halibut lay near the bait prior to initiating a bait attack, most either directly downstream or to one side of the bait in relation to the current. This behavioral response may reinforce olfactory clues that led the fish to the bait, or possibly a restrained response to the baited hook as a novel prey item (Løkkeborg, 1990). Rejection of the bait at this point was often followed by looping, behavior that often led to further bait interaction. The role of mechanoreception was not demonstrated. In only a few instances did halibut exhibit incomplete bites, and these generally did not result in the fish then leaving the area of the gear. Most bites were associated with extremely active behavior, e.g. a fish beginning to rush simultaneously with biting the bait. Only one bite that resulted in hooking was not followed by a rush.

In the simplest interpretation, the attack rate for halibut was 43%. Fish length was not a significant

factor in attack rate, although approach direction was highly significant; fish that approached the bait upstream bit almost twice as often as fish that approached from the side or downstream, and four times as often as fish that approached during slack current. It is likely that fish approaching upstream were following a scent trail from the baits and had a higher motivation to bite than fish that approached from other directions.

It is interesting to note that although halibut appeared throughout the gear deployment, consistent with the idea of being aroused by and following a scent plume from different distances, once a fish arrived at the area of the baited hooks, bait attacks occurred quickly. Most attacks occurred within the first minute after a halibut appeared, and less than five percent of the bait attacks occurred more than one and one-half minutes after the fish appeared.

Postbiting behavior and hooking success

In almost all cases, complete bites were followed by rushing behavior, which resulted in about equal numbers of hooked fish and fishes that spat the hook and then departed the observation area. Hooked fish struggled violently for a short period, then went into a series of resting and rushing behaviors which continued through the observation period, the duration of rushes becoming gradually shorter.

Size selectivity by hook-and-line gear has a number of components, including encounter rate, attack rate, and hooking success. A higher encounter rate has been shown for larger fish, which may have greater foraging ranges and therefore a higher probability of encountering baited gear (Løkkeborg and Bjordal, 1992; Engås and Løkkeborg, 1994; Bjordal and Løkkeborg, 1996). It is possible that the present experimental arrangement was skewed in this way toward catching larger halibut. Attack rate has been related to bait size for some species; larger fish show a preference, and therefore a higher attack rate, for larger baits, and smaller fish showing a preference for smaller baits (Bjordal and Løkkeborg, 1996). No difference in attack rate by fish size was seen in the present study.

Hooking success was found to be strongly dependent on fish length, ranging from zero for fish less than 62 cm, to 83% for fish 93–97 cm (Fig. 5). This finding is consistent with and can explain much of the selectivity estimated from representative IPHC commercial and setline survey data (Clark[1]). A circle

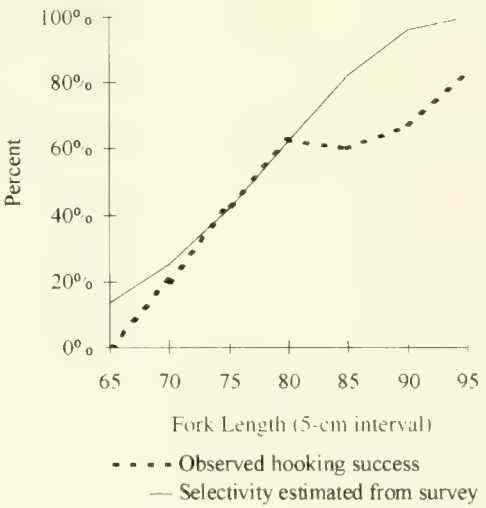

Figure 5

Hooking success from direct observation and selectivity estimated from IPHC survey data by 5-cm length groups.

hook is designed so that it is pulled to the corner of the mouth during rushing, with the point of the barb in line with the pull of the gangion (Bjordal and Løkkeborg, 1996). Hooking results from the orientation of the hook during the rush and the penetration of the barb caused by the pull on the gangion during that rush, the point of the hook circling the jawbone and exiting through the cheek (Johannes, 1981). Ninety to ninety-five percent of halibut caught on circle hooks are hooked in this manner (Kaimmer and Trumble, 1997).

Hooking success has been related to hook size only when the range of hook sizes is very great, on the order of 200% or more (Løkkeborg and Bjordal, 1992) and has been explained in terms of larger fish being able to exert a stronger pull on the gangion during rushing. This stronger pull generates the greater force necessary to pull the point of a larger hook fully into the tissue of the mouth cavity, resulting in a higher rate of hooking success. A greater hooking success as the result of a larger fish exerting a stronger pull may be countered by weaker tissue in the mouth of smaller fish, requiring less force for the hook to penetrate (Bjordal and Løkkeborg, 1996). The hooking success table (Table 4) in this study was constructed for fish 62–97 cm in length, the largest just 1.5 times the length of the smallest, and showed dramatic differences in hooking success over length changes as small as 10–20 cm. Some mechanism beyond pull strength was probably responsible for these differences. In an earlier study where the same hooks

[1] Clark, W. 1997. Coastwide distribution of exploitable biomass according to 1997 setline surveys. Int. Pac. Halibut Comm. Rep. of Assessment and Research Activities, p. 161–202. International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98105-2009. Unpubl. manuscript.

(Kaimmer, 1994) were used, halibut less than 82 cm in length were hooked more often in locations other than the jaw than were larger halibut. Although this difference was small, it suggests a functional relation between the mechanical operation of the hook and the size of the fish's mouth in relation to overall hook and bait dimensions. A higher rate of hooking success for smaller halibut might have been seen if smaller bait had been used. This was not tested in the present experiment because bait size was held constant to the standard used in IPHC setline surveys and representative of the commercial halibut fishery.

It is clear that an increased hooking success for larger fish has a dramatic effect on the size selection of longline gear. Much of the length-based selectivity assumed for halibut setlines can be explained by the differences in hooking success by fish length demonstrated by this study. The selection curve generated from the present observations is the first to be determined for Pacific halibut through direct observation of hook attacks.

Conclusions

We consider the results of this study to be qualitative, not quantitative. Their application to commercial or experimental longline sets or CPUE indices should take into account the limited nature of the experiment, both in terms of number of hooks fished and in terms of lack of seasonal or wide areal variation in the observations. Although it is likely that the results are generally applicable to halibut, they could vary significantly for fish with different feeding histories in a different life stage. Attack rate particularly could be susceptible to the condition of fish in relation to recent feeding or spawning activity. The primary objective of this project was to determine estimates for the attack rate and hooking success of Pacific halibut on gear typical of those used in the commercial fishery. Results show that although these parameters may be estimated, their values are influenced by a number of factors, most notably by the presence of bottom current and direction of approach in relation to that current (for attack rate) and fish length (for hooking success). The behavioral sequences observed for Pacific halibut were fairly limited and included searching into a current for food, looping and lying around or near bait items, and a vigorous biting–rushing sequence that often resulted in hooking. The relative absence of physical contact with the bait prior to biting (such as tasting) might indicate that texture is less important for food selection by halibut. The role of vision in halibut feeding was not tested.

The large number of bait attacks by species other than halibut compensated for the very low hooking success for these species. In fact, we caught more of these species than halibut during the experiment. Although their presence or interaction with baits short of hooking did not seem to affect the attack rate of halibut that were present, the removal of available baits by interspecies competition should be included in any model of hook-and-line CPUE.

Acknowledgments

The author expresses his thanks to S. Løkkeborg for comments on an early draft of this paper, as well as three anonymous reviewers who gave many useful suggestions. I would also like to thank Craig Rose and Scott McIntire, National Marine Fisheries Service, Seattle, for loan of the camera gear and for invaluable assistance in training me in its use, and most especially for their long-distance troubleshooting during the project.

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Mitochondrial DNA analysis of population structure in the Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae)

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Abstract.—Genetic population structure in Atlantic croaker (*Micropogonias undulatus* Linnaeus) was examined by using the polymerase chain reaction (PCR) and restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Juvenile croaker from three U.S. Atlantic localities (Delaware, North Carolina, and Florida) and one Gulf of Mexico locality (Louisiana) were screened to document the magnitude and spatial distribution of mtDNA variation in *M. undulatus*; to evaluate the integrity of Cape Hatteras, North Carolina, as a genetic stock boundary; and to estimate levels of gene flow among Atlantic localities to provide an improved basis for future decisions regarding coastwide management of this fishery resource.

RFLP analysis of the ATPase 6 and D-loop mtDNA regions revealed a total of 15 composite haplotypes in 93 individuals. Monte Carlo simulations revealed no geographic heterogeneity in mtDNA haplotype frequencies among Atlantic localities and no evidence that juveniles collected north and south of Cape Hatteras originated from separate gene pools (net sequence divergence=–0.002%). There was significant heterogeneity between Atlantic and Gulf of Mexico samples, suggesting restricted gene flow between these two regions. Analysis of molecular variance also indicated regional (Atlantic versus Gulf) population structure, but provided no evidence that Cape Hatteras represents a genetic stock boundary. AMOVA indicated relatively high gene flow ($N_f m_{\perp}$ = 12–23 effective female migrants per generation) among Atlantic localities. These findings are consistent with 1) a single genetic stock of *M. undulatus* on the Atlantic coast and 2) separate, weakly differentiated stocks in the Atlantic and Gulf of Mexico.

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Fish. Bull. 97:884–890 (1999).

Atlantic croaker (*Micropogonias undulatus* Linnaeus) is an important commercial and recreational fishery species along the U.S. Atlantic and Gulf of Mexico coasts (Chao and Musick, 1977; Mercer[1]). On the Atlantic coast, *M. undulatus* is common in estuarine and coastal waters from Indian River, Florida, to Chesapeake Bay (Nelson et al., 1991; Stone et al., 1994). Current fishery management practices for *M. undulatus* assume a single or "unit" stock for the entire Atlantic coast (Kline and Speir, 1993) despite indications that two stocks may exist. The two-stock hypothesis is based on variation in life history traits and population dynamics of Atlantic croaker occurring north and south of Cape Hatteras, North Carolina. White and Chittenden (1977) reported lower mortality rates, greater longevity, and larger maximum size for *M. undulatus* north of Cape Hatteras. Ross (1988) concluded that two groups with contrasting life histories may overlap in the vicinity of Cape Hatteras, with the northern, mainly offshore group exhibiting greater size-at-age, greater longevity, lower annual mortality, and delayed maturation compared with southern individuals. Geographic variation in biological characteristics of northern and southern *M. undulatus* implies that these groups may respond independently to exploitation and may require management as separate stocks; however, the basis for these differences (i.e. genetic or ecophenotypic) is unclear.

Identification of Atlantic croaker stock structure was listed among the priority research needs by the 1981 Sciaenid Assessment Workshop sponsored by the Atlantic States Marine Fisheries Commission (ASMFC) and National Marine Fisheries Service (Wilk and Austin, 1981). The Atlantic Croaker Fishery Management Plan, prepared under the ASMFC Interstate Fishery Management Program, also recommended research to identify croaker stocks along the Atlantic coast (Mercer[1]). In the present study, polymerase chain reaction (PCR) and restriction fragment length polymorphism analysis

[1] Mercer, L. P. 1987. Fishery management plan for Atlantic croaker. Fisheries Management Rep. 10, Atlantic States Marine Fisheries Commission, Washington, D.C., 90 p.

Table 1

Sampling localities for juvenile Atlantic croaker. *n* is the number of individuals assayed from each locality.

Region and locality	Site	Collection date	*n*	Standard length (mm) mean (SD)	Standard length (mm) range
Atlantic					
Delaware Bay, Delaware (DE)	38°48'N 75°10'W	Oct 94	23	17.1 (1.8)	13–20
Cape Fear River, North Carolina (NC)	33°58'N 78°01'W	May 93	24	16.0 (1.9)	13–19
Indian River, Florida (FL)	28°03'N 80°35'W	Mar 94	22	19.4 (2.2)	16–23
Gulf of Mexico					
Terrebonne Bay, Louisiana (LA)	29°10'N 90°30'W	Jul 96	24	89.4 (4.5)	79–98

(RFLP) were used 1) to document the magnitude and spatial distribution of mtDNA variation in *M. undulatus* from U.S. Atlantic and Gulf of Mexico localities, 2) to evaluate the integrity of Cape Hatteras, North Carolina, as a genetic stock boundary, and 3) to estimate levels of gene flow among Atlantic localities to provide an improved basis for future decisions regarding coastwide management of this fishery resource.

Methods

Juvenile Atlantic croaker were collected from three U.S. Atlantic estuaries (Delaware Bay, Cape Fear River, and Indian River Lagoon) and one Gulf of Mexico estuary (Louisiana) (Table 1). Sampling localities were chosen to represent the northern, central, and southern portions of the species' U.S. Atlantic coast range and to include areas north and south of the hypothesized stock boundary at Cape Hatteras, North Carolina.

Genomic DNA extracts from individual croaker were obtained by using the Puregene DNA isolation kit (Gentra Systems, Inc., Minneapolis, MN) and were used in the polymerase chain reaction (Saiki et al., 1988) to amplify two mtDNA regions: the protein-coding ATP synthetase subunit 6 gene (ATPase 6) and the noncoding "D-loop" segment of the control region (Lankford, 1997). ATPase 6 was amplified by using the primers ATPase 6-L and ATPase 6-H (Quattro[2]), which yielded a 705-base-pair (bp) product. Primers L-Thr (5'-3': AGC TCA GCG CCA GAG CGC CGG TCT TGT AAA) and 12SAR-H (5'-3': ATA GTG GGG TAT CTA ATC CCA GTT) were used to amplify a 1540-bp product containing the entire D-loop region, tRNA-Pro and tRNA-Phe genes, and portions of the 12S rRNA and tRNA-Thr genes (Lee et al., 1995). Amplifications were performed in 50 μL reaction volumes according to Kocher et al. (1989). PCR products were digested with twelve restriction endonucleases: *Hinf*I, *Hae*III, *Msp*I, *Pvu*II, *Sau96*I, *Alu*I, *Mse*I, *Rsa*I, *Taq*I, *Dde*I, *Nla*III, and *Hha*I (obtained from New England BioLabs, Beverly, MA) (Lankford, 1997). Variant RFLP patterns were confirmed by means of repeat digestions and electrophoresis on 3% NuSieve agarose gels. Fragment sizes were estimated by using molecular weight markers: pUC18-*Hae*III digest from Sigma-Aldrich Corp., St. Louis, MO, pBR322-*Msp*I digest from New England BioLabs, Beverly, MA, and pBR322-*Bst*NI digest from New England BioLabs; and the ANAGEL software program (Mrazek and Spanova, 1992).

Distinctive restriction-fragment patterns were identified by letter codes and subsequently combined to produce composite mtDNA haplotypes for individual fish. Nucleon diversity (h) was calculated for each locality (Nei and Tajima, 1981) with standard errors estimated according to Nei (1987). Nucleotide sequence diversity and nucleotide sequence divergence were calculated with the Restriction Enzyme Analysis Package (REAP, version 4.0) (McElroy et al., 1992). Frequency distributions of composite mtDNA haplotypes were tested for geographic homogeneity by using a Monte Carlo chi-square simulation approach (Roff and Bentzen, 1989) and a total of 10,000 random data resamplings. The integrity of Cape Hatteras as a genetic stock boundary was tested by comparing mtDNA haplotype frequencies north (Dela-

[2] Quattro, J. M. 1996. Department of Biological Sciences, Univ. South Carolina. Personal commun.

ware) and south (North Carolina and Florida) of this locality. Phylogenetic analysis was employed by using the character-state approach to construct a maximally parsimonious network relating individual haplotypes based on the number of restriction-site differences (Avise, 1994). The resulting network was examined for geographic structuring of haplotypes within and among sampling regions.

Population structure in *M. undulatus* was also evaluated by using nested analysis of molecular variance (AMOVA [Excoffier et al., 1992]). AMOVA input consisted of an Euclidean distance matrix containing genetic distance values for all possible pairs of the 15 observed mtDNA haplotypes. Samples were stratified by locality (DE, NC, FL, and LA) and nested within region (Atlantic or Gulf). Total genetic variation was partitioned into three components: within geographic localities, among geographic localities within the Atlantic region, and between regions. Significance of variance components was tested by using 10,000 random permutations to generate null distributions for each variance component. Gene flow among localities was estimated with Wright's (1943) island model, modified for mtDNA: $F_{ST} = 1/2N_e m_{\varphi} + 1$. Calculations employed Φ_{ST} as an approximation of F_{ST}.

Results

RFLP analysis of the ATPase 6 and D-loop regions revealed a total of 68 restriction sites. The average individual was scored for 62 sites and 264 nucleotide positions representing approximately 12% of the ATPase 6 and D-loop regions combined, or 1.6% of the entire mitochondrial genome. A total of 15 composite haplotypes was detected in *M. undulatus* (Table 2). Of the 93 individuals surveyed, 67 (72%) shared the same composite genotype (haplotype 1). Genetic distance among haplotypes averaged 0.17% for the pooled sample, with the most divergent haplotypes (10 and 12) differing from the common haplotype by only 0.75% and 1.0%, respectively.

Nucleon diversity (h) averaged 0.47 ±0.01 (mean ±SE) for the pooled sample, and ranged from $h = 0.25$ ±0.12 in DE to $h = 0.62$ ±0.12 in LA. Nucleotide sequence diversity also varied geographically, ranging from $\pi = 0.07\%$ in DE to $\pi = 0.32\%$ in LA. Net sequence divergence (p) among localities was low, indicating that most of the observed mtDNA variation occurred within localities. Average sequence divergence for the pooled sample was $p = 0.004\%$, with comparisons among Atlantic localities yielding slightly lower divergence values than comparisons involving Gulf and Atlantic samples. Croaker collected north versus south of Cape Hatteras were genetically indistinguishable (p=–0.002%) whereas nucleotide divergence between regions (pooled Atlantic vs. Gulf) was 0.005%.

Table 2

Geographic distribution (see Table 1 for specific locations) of composite mtDNA haplotypes among Atlantic croaker samples from Atlantic and Gulf of Mexico localities. Letters denote mtDNA fragment patterns (lowercase = ATPase 6; uppercase = D-loop) produced by digestion of PCR products with the following polymorphic restriction endonucleases: ATPase 6: *Pvu*II, *Alu*I, *Dde*I; D-loop: *Hinf*I, *Hae*III, *Msp*I, *Mse*I, *Taq*I, *Nla*III, *Hha*I.

Composite mtDNA haplotype	Haplotype frequency				
	DE	NC	FL	LA	Total
1. aaaAAAAAAA	20	16	16	15	67
2. bbaAAAAAAA	1	1	0	2	4
3. aaaAAAACAA	1	1	2	0	4
4. aaaAAAABAA	1	3	0	0	4
5. aaaAAAAAAB	0	1	0	0	1
6. aaaDAAAAAA	0	1	0	0	1
7. aaaABAAAAA	0	1	0	1	2
8. aaaBAAAAAA	0	0	3	0	3
9. aaaAAABAAA	0	0	1	0	1
10. aaaAAAABBC	0	0	0	1	1
11. aaaAAAAABA	0	0	0	1	1
12. aaaBBAAAAC	0	0	0	1	1
13. aaaAABAAAA	0	0	0	1	1
14. aabAAAAABA	0	0	0	1	1
15. aaaAAAAAAC	0	0	0	1	1
Totals	23	24	22	24	93

The common mtDNA genotype (haplotype 1) was numerically dominant at all localities (Table 2). The remaining 14 haplotypes occurred at low (<10%) frequencies. Monte Carlo tests for homogeneity revealed no significant heterogeneity in mtDNA haplotype frequency distributions within the SAB (NC vs. FL, χ^2=11.3, p=0.140) or among all Atlantic localities (p=0.148). When NC and FL samples were pooled and compared to the DE sample, there was no indication of heterogeneity among samples collected north and south of Cape Hatteras (χ^2=4.6, p=0.906). To further test for population structure within the Atlantic region, an additional 20 specimens from each Atlantic locality were screened for D-loop variation with the polymorphic enzymes *Taq*I and *Hha*I. Neither *Taq*I (χ^2=3.45, p=0.562) nor *Hha*I (χ^2=1.95, p=0.682) haplotype frequencies exhibited significant heterogeneity among Atlantic localities.

Given the lack of heterogeneity within the Atlantic region, composite haplotype frequencies were pooled across Atlantic localities and compared with the Gulf of Mexico sample. Monte Carlo simulations

Table 3

Hierarchical nested analysis of molecular variance on genetic distance between Atlantic croaker mtDNA haplotypes.

Variance component	df	Φ statistic	Variance	% total	P
Among regions (Atlantic vs. Gulf)	1	$\Phi_{CT} = 0.046$	0.021	4.6	<0.01
Among localities within Atlantic	2	$\Phi_{SC} < 0.001$	<0.001	<0.1	0.10
Within localities	89	$\Phi_{ST} = 0.046$	0.431	95.4	0.03

revealed significant heterogeneity between Atlantic and Gulf samples (χ^2=24.36, p=0.020) (Table 2). Parsimony analysis indicated that geographically segregated haplotypes were generally closely related (1–2 restriction site changes) to the common haplotype (Fig. 1). AMOVA revealed that the majority (95.4%) of mtDNA variation in Atlantic croaker occurred within samples (Table 3). A significant portion (4.6%) was attributable to regional differences (Atlantic versus Gulf, P<0.01) but variation within the Atlantic region was unstructured (p=0.10) and accounted for <0.1% of the total genetic variance. Φ_{ST} values indicated a lack of geographic structure and relatively high gene flow among Atlantic localities. Gene flow among Atlantic localities was estimated as 23.4 (DE and NC), 16.8 (NC and FL), and 12.0 (DE and FL) effective female migrants per generation.

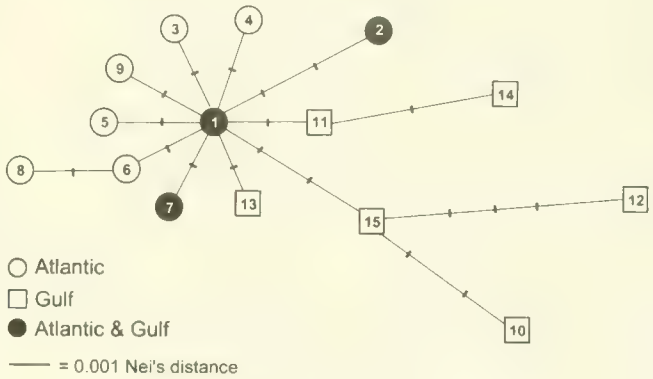

Figure 1

Parsimony network relating 15 mtDNA haplotypes observed in Atlantic croaker. Hatch marks drawn through each branch indicate the inferred number of restriction site differences among haplotypes. Branch lengths denote Nei's genetic distance between haplotypes (note scale).

Discussion

MtDNA analysis provided no evidence that *M. undulatus* is subdivided by Cape Hatteras into discrete genetic stocks. Frequency- and distance-based analyses both suggested a single, panmictic population of croaker on the U.S. Atlantic coast. Low levels of mtDNA divergence among Atlantic localities, although not statistically significant, were more consistent with a pattern of semi-isolation by distance rather than marked subdivision by Cape Hatteras. For example, AMOVA revealed that the two Atlantic localities exhibiting the least genetic divergence were DE and NC (Φ_{ST}=0.021; p=0.89). NC and FL samples were slightly more divergent but not significantly so (Φ_{ST}=0.029; p= 0.180). Lack of population structure was perhaps best indicated by the lack of differentiation between DE and FL samples (Φ_{ST}=0.040; p=0.084), two locations representing the distributional limits of this species' range on the U.S. Atlantic coast.

Kornfield and Bogdanowicz (1987) inferred patterns of gene flow from distributions of unique mtDNA haplotypes and their presumed precursors, predicting that under restricted gene flow, unique haplotypes should occur in the same population as their precursors. This was the case for *M. undulatus* at the regional (i.e. Atlantic versus Gulf) level, where unique Gulf haplotypes 10, 12, and 14 each had likely precursors that were confined to the Gulf region. Within the Atlantic region, however, unique haplotypes and their likely precursors occurred at disparate localities. The occurrence of rare haplotypes at more than one Atlantic locality also implies that genotypes arising at one locality spread rapidly to other localities within the Atlantic. Combined with low levels of nucleotide divergence, these observations support the hypothesis of contemporary gene flow among Atlantic localities. Gene flow estimates based upon Wright's island model are consistent with panmixia: values ranged from $N_e m$ =12.0–23.4, well above the theoretical lower limit of $N_e m$ = 1 sufficient to preclude genetic divergence of populations by random drift (Slatkin, 1985).

Previous studies have reported geographic variation in life history traits and population dynamics of Atlantic croaker found north and south of Cape Hatteras (White and Chittenden, 1977; Ross, 1988), suggesting that two groups of croaker with contrasting life histories overlap in the Cape Hatteras region, with a mainly offshore group north of Cape Hatteras which displays greater size-at-age, greater longevity, lower annual mortality, and delayed maturation in relation to croaker south of Cape Hatteras. A more recent study by Barbieri et al. (1994a) in the Chesapeake Bay concluded that life history variation in *M. undulatus* was ephemeral and that the two-stock hypothesis should be re-evaluated. The present mtDNA analysis supports previous suggestions by Ross (1988) and White and Chittenden (1977) that life history variation, when present, has an ecophenotypic basis.

A review of *M. undulatus* life history characteristics lends support to the panmixia hypothesis for the Atlantic region and provides several mechanisms by which trans-Hatteras gene flow may occur. Mark–recapture studies indicate extensive movement by *M. undulatus* along the U.S. Atlantic coast and thus potential for gene flow by means of adult migration (Pearson, 1932; Haven, 1959; Bearden, 1964; DeVries[3]). Larval dispersal could augment gene flow. Atlantic croaker larvae are abundant at outer-continental shelf locations (Govoni and Pietrafesa, 1994) and may spend more than 60 days in shelf waters before reaching estuaries (Warlen, 1980). Offshore spawning combined with an extended pelagic larval stage in shelf waters could provide ample opportunity for larval dispersal among Atlantic localities. Interestingly, spring recruits are occasionally reported in the mid-Atlantic Bight (MAB) estuaries as late as May and June (Haven, 1957; Chao and Musick, 1977) despite reports that spawning ceases in this area by late December (Morse, 1980; Barbieri et al., 1994b). Spring recruits to MAB estuaries may therefore be transported to mid-Atlantic estuaries from spawning sites south of Cape Hatteras. Thorrold et al. (1997) found no significant differences in otolith chemistry of juvenile croaker from the Neuse River, North Carolina, and the Elizabeth River, Virginia, suggesting that immigrants to estuaries north and south of Cape Hatteras may originate from the same spawning area. The reproductive strategy of *M. undulatus* may also facilitate gene flow. Atlantic croaker are multiple spawners with indeterminate fecundity (Barbieri et al., 1994b). Because spawning occurs during a southerly coastal migration during fall, females could commence spawning within the MAB and spawn multiple times during their southward migration, effectively distributing maternal half-siblings (mtDNA clones) over an extensive geographic range.

MtDNA heterogeneity between Atlantic and Gulf of Mexico localities suggests that these regions support separate populations of *M. undulatus*. The observed genetic break is consistent with a contemporary range discontinuity in southern Florida, where *M. undulatus* seldom occur south of Indian River on the Atlantic coast and are rarely encountered south of Tampa Bay on the Gulf coast (Nelson et al., 1991; Pattillo et al., 1997). Average sequence divergence between Atlantic and Gulf haplotypes (p=0.005%) was relatively low, however, suggesting that the phylogenetic break between Atlantic and Gulf stocks may be less pronounced in *M. undulatus* than in other marine fishes (Bowen and Avise, 1990).

This study represents the first attempt to identify population genetic structure in *M. undulatus* using DNA-level markers. The technique employed in our study proved sufficiently powerful to detect regional (Atlantic vs. Gulf of Mexico) population structure, but did not reveal structured genetic stocks of croaker within the Atlantic. The integrity of Cape Hatteras as a genetic stock boundary could be tested further by using fine-scale markers such as microsatellites, which have revealed genetic differentiation among fish populations that exhibit little mtDNA divergence. Alternatively, higher-resolution mutation-screening analysis or direct sequencing of the mitochondrial D-loop region might provide greater resolution of geographic structure than the RFLP technique employed here (Ong et al., 1996; Stabile et al., 1996).

Although mtDNA analysis did not indicate discrete genetic stocks of croaker within the Atlantic region, harvest stocks (see Gauldie, 1988) worthy of management consideration may exist. Because low levels of gene flow may produce mtDNA homogeneity between otherwise self-recruiting stocks, mtDNA is incapable of distinguishing between low (1%) and moderate (50%) amounts of mixing (Carvalho and Hauser, 1995). Delineation of harvest stocks will thus require more precise estimates of mixing than those obtainable from mtDNA analysis. Mark–recapture studies designed to quantify the level of adult migration across Cape Hatteras, combined with otolith-based microchemical analyses to examine larval dispersal patterns, could provide valuable information on the level of mixing between the MAB and South

[3] DeVries, D. A. 1986. Inshore Atlantic croaker tagging study. *In* J. L. Ross, D. A. DeVries, J. H. Hawkins III, and J. B. Sullivan, Assessment of North Carolina commercial finfisheries, p. 331–394. Completion report for Project 2-386-R, North Carolina Department of Natural Resources and Community Development, Div. Marine Fisheries, Morehead City, NC.

Atlantic Bight (SAB) areas and clarify the extent to which *M. undulatus* in these regions constitute self-recruiting groups.

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Otolith microstructure, age, and growth patterns of dolphin, *Coryphaena hippurus*, in the western Mediterranean

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Abstract.—The age and growth of dolphin, *Coryphaena hippurus*, has been determined in wild specimens between 14.4 and 124 cm fork length (FL) caught off Majorca (Balearic Islands, western Mediterranean). Also, several methods have been applied to validate the results obtained and to assess the aging techniques presently used. In accordance with the sexual dimorphism of this species, the length–weight relationship showed negative allometry in females and isometry in males. The high correlation between increment counts and known age in 75 reared larvae from 0 to 38 days old (number of increments = 0.3894+0.9846·days of age; r=0.98) indicated that the daily deposition of growth increments in sagittal otoliths and regular incremental formation begins on day one. This correlation validated the use of otoliths in the aging of 176 juvenile specimens between 16.5 and 58.5 cm FL, in which the minimum and maximum ages observed were 47 and 176 days, respectively. Nevertheless, the progressive increase in complexity with the ontogenic development of these structures suggests that this method may underestimate age in adult fish, probably owing to the loss of marginal zones of the otolith during the polishing process. Thus, from 150 specimens between 65 and 124 cm FL, the interpretation of annuli from scales gave ages up to 3 years old, whereas readings of otoliths in 36 specimens of the same size interval gave ages between 0 and 1 year old. Growth parameters were calculated from the age–length relationships of otolith and scale readings in juvenile and adult fish, respectively, and from the analysis of monthly length-frequency distributions, obtained in 1990 and 1991 during the exploitation of juveniles from 18 to 70 cm FL (n=4084). The values obtained for L_∞ ranged from 72.4 cm FL in unsexed juveniles and 110.0 cm FL in females both juvenile and adult, whereas k ranged from 1.6/year in juvenile and adult females and 2.5/year in unsexed juveniles. Although the results obtained were quite different owing to the different length and age range considered, similar results were obtained by comparing the growth performance index (F), and showed the rapid growth of the species.

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Fish Bull. 97:891–899 (1999).

Dolphin (*Coryphaena hippurus* Linnaeus, 1758) (Pisces: Coryphaenidae) is an epipelagic, top-level predator species widely distributed in the tropical regions of every ocean (Palko et al., 1982). It migrates widely, and in warmer months increases its range to subtropical areas. Thus, it occurs seasonally in the Mediterranean from spring to autumn, when surface waters reach temperatures above 16–18°C (Massutí and Morales-Nin, 1995); mature specimens are occasionally caught in the swordfish (*Xiphias gladius*) fishery with surface longlines at this time, and immature juvenile fish are exploited by small-scale fisheries that deploy surrounding purse nets around fish aggregation devices.

Dolphin age and growth have been determined by means of scale annuli (Beardsley, 1967; Rose and Hassler, 1968), daily growth increments in otoliths (Oxenford and Hunte, 1983; Uchiyama et al., 1986), and modal progression analysis (Wang, 1979; Murray, 1985). In addition, some growth studies have been made of fish of known age reared in captivity (e.g. Hassler and Hogarth, 1977; Ostrowski et al., 1989; Benetti et al., 1995b). In the Mediterranean, available growth data on this species are related to morphometric relationships (Lozano-Cabo, 1961; Bannister, 1976) and rearing experiments (Reñones et al., 1992; Ayari et al., 1995).

The objective of this paper was to determine, for the first time in the Mediterranean, the age and growth patterns (including juvenile and adult phases) of *C. hippurus*. To support age and growth parameters estimated from readings of scales and otoliths, direct validation by means of rearing experiments and indirect validation based on length-frequency analysis were also applied. Otolith microstructure was analyzed to determine increment patterns and morphological changes during growth and to obtain more precise increment counts.

Material and methods

From May to November 1990 and 1991, fork lengths (FL) of adult specimens (n=150) were measured from longline catches. Sex was determined on the basis of the sexual dimorphism of the species (Palko et

al., 1982). Scales were collected above the lateral line, at the level of the pectoral fin, cleaned with 5% KOH, and mounted on slides. Interpretation of scale rings was carried out with a projector at 10× magnification by using the method described by Beardsley (1967). The scarcity of adult fish prevented the use of age validation methods; therefore the annual nature of the rings was established from validated ages from other areas (Beardsley, 1967; Rose and Hassler, 1968). Juvenile fish (n=4084) were measured from 65 samplings made between August and December of the same years from small-scale fishery catches. Total weight and sex were recorded for subsamples (adults n=68, juveniles n=282) selected to cover the size distribution of both sexes. Sagittal otoliths were removed, cleaned, and stored in distilled water. Unbroken otoliths (n=212) were embedded in epoxy resin and polished with a graded series of sandpaper and, finally, with 0.3-µm alumina paste. To improve clarity, otoliths were moistened with immersion oil for several hours before reading.

Otoliths have a complex structure, with convex sides, pronounced rostrum and antirostrum, and a demarcated sulcus that terminates in a V-shaped excisural notch (Oxenford and Hunte, 1983). We selected the dorsal side of the otolith to obtain a section with a complete increment sequence. Otoliths were read under a light microscope coupled to a high-resolution video camera and monitor system. Growth increments were counted from the core to the edge of the pararostrum (Oxenford and Hunte, 1983). Incremental counts were made by beginning at the first clearly defined mark that encircled the primordium, which defines the outer edge of the nucleus. Growth increments in juvenile fish otoliths were enumerated along a single axis. In adult fish it was necessary, however, to follow a circuitous path to complete a set of counts, following prominent increments laterally until an area with clear increments was found. Each otolith was read independently by two of the authors; results were accepted only if the readings were coincident or their difference was less than 5%. Growth increments were counted at 500× and verified at 1000×. Microstructural growth increments were studied on fish of 22–43 cm FL (n=28) with a scanning electron microscope (SEM). To highlight increment zones, the polished sections were etched for 30 seconds with a 0.1 N HCl solution, or for 60–90 seconds with a 0.2 M EDTA solution.

Von Bertalanffy growth parameters were estimated from age–length relationships obtained from scale and otolith readings by using the FISHPARM program (Prager et al., 1987). These parameters were validated by an independent length-based method by using the ELEFAN I procedure included in the ELEFAN software package (Gayanillo et al.[1]). Because L_∞ and k are inversely correlated, the growth performance index ($\Phi = 2\log L_\infty \log k$) was employed to compare growth rates (Munro and Pauly, 1983).

The temporal relation between ring number and age was determined by using larvae of known age, obtained from eggs spawned in captivity. Larvae hatched on 25 July 1994 and were reared through the juvenile stage up to 38 days, according to the method described by Kraul (1989). Water temperatures during the experiment ranged from 26° to 27°C, within the range of water surface temperature found around the Balearic Islands from June to August, when the species spawns (at 24–27°C; Massutí and Morales-Nin, 1995). The presence of early larval stages has also been reported in the study area during this period (Alemany and Massutí, 1998).

To establish the timing of first ring deposition and early otolith growth, larvae were sampled daily during the first 15 days. Afterwards, three samples were taken at intervals of 7–8 days until the juveniles were 38 days old. Larvae were preserved in buffered alcohol. The standard length (SL) of each larva was measured, and sagittal otoliths (n=93) were removed, cleaned, and mounted on slides with epoxy resin. The otoliths were read with an image analysis system connected to a microscope. An iterative semiautomatic system was employed for detection of increments, measurement of otolith radius, and age attribution. Increment clarity was improved by using polarized light, and enhanced digitized images were used for interpretation. Each otolith was read at least twice at 1000× magnification with an oil lens.

Daily periodicity of increments in reared specimens was validated by linear regression analysis of the relation between counts of otolith increments and days. The intercept and the slope were examined with Student's t-test. This method was also used to test the isometry in the allometric indices obtained by applying exponential regression equations to the length–weight relationships.

Results

The parameters of the length–weight relationship for females, males, and the whole population, including unsexed specimens, are shown in Table 1. Isometric growth was found in males (t-test; P>0.05), but for females and the population as a whole, a negative allometry was found (t-test; P<0.01).

[1] Gayanillo, F. C., M. Soriano, and D. Pauly. 1988. A draft guide to the complete ELEFAN. ICLARM Software Project 2, 70 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Table 1

Length–weight relationship parameters estimated by exponential regression equations ($y = ax^b$) between fork length (cm) and total weight (g) in *Coryphaena hippurus*. n = number of specimens; SE = standard error of slope; r = correlation coefficient.

Population	n	a	b	SE	r
Females	192	0.0139	2.8983	0.0011	0.997
Males	154	0.0092	3.0187	0.0018	0.996
Total	350	0.0113	2.9605	0.0007	0.996

The sagittae of *C. hippurus* are small in relation to fish size and generally butterfly-shaped, although they display different structural patterns with ontogenic development. The larval otoliths are round and the development of the rostrum starts at 8 days (Fig. 1, A and B). The sulcal structure is formed in 12-day-old larvae (Fig. 1C); the rostrum and antirostrum were, on average, separated in 17-day-old larvae (Fig. 1D).

Otoliths prepared for SEM observation showed differences depending on the etching agent. The otoliths etched with EDTA had less clear growth increments than did otoliths etched with HCl. These differences might be due to high protein content in the otoliths, which collapsed when the aragonite crystals were completely removed with EDTA. Whole otoliths showed the presence of concentric laminations or ridges (Fig. 2A) which revealed that the core region grew by the deposition of successive layers on the inner side. Sections of otoliths showed the typical pattern of incremental and discontinuous units, which formed growth increments with variable widths depending on the otolith area (Fig. 2, B and C). Some rhythmic patterns were also evident with 7–14 increment groupings (Fig. 2, B and D).

Under the light microscope, otoliths revealed a pattern of alternating light and dark concentric rings surrounding a core, which was deposited at the earliest stages of development (Fig. 3A). The width of the increments varied from the core to the edge, with narrow increments near the center of the otolith and at the edge, whereas wider ones were laid down from the first to the third month of life (Fig. 3, B and C). These differences in increment width may reflect periods of differential growth. Larger increment patterns, or bands composed of groups of 7–14–28 increments, were also observed (Fig. 3B), suggesting lunar growth rhythms.

From 93 reared larvae of known age, a total of 75 otoliths (81%) could be read under the light microscope. These larvae measured 3.8–65.0 mm SL, and their otolith radii ranged from 10.7 mm (at day 0,

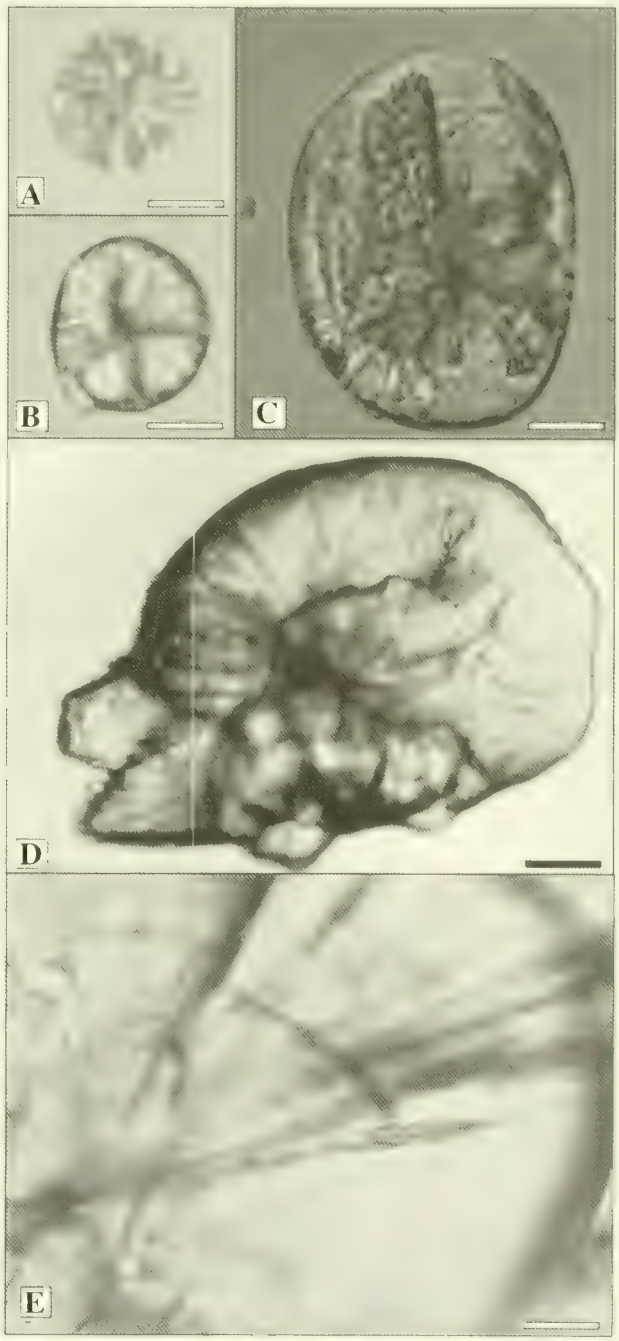

Figure 1

Photomicrographs of sagittal otoliths from *Coryphaena hippurus* larvae reared in captivity: (**A**) 6-day-old larvae of 6.1 mm SL (scale bar=25 μm); (**B**) 8-day-old larvae of 8.5 mm SL (scale bar=29 μm); (**C**) 12-day-old larvae of 8.8 mm SL (scale bar=34 μm); (**D**) 17-day-old larvae of 30 mm SL (scale bar=56 μm). (**E**) Poorly defined increments laid down around the core (scale bar=90 μm).

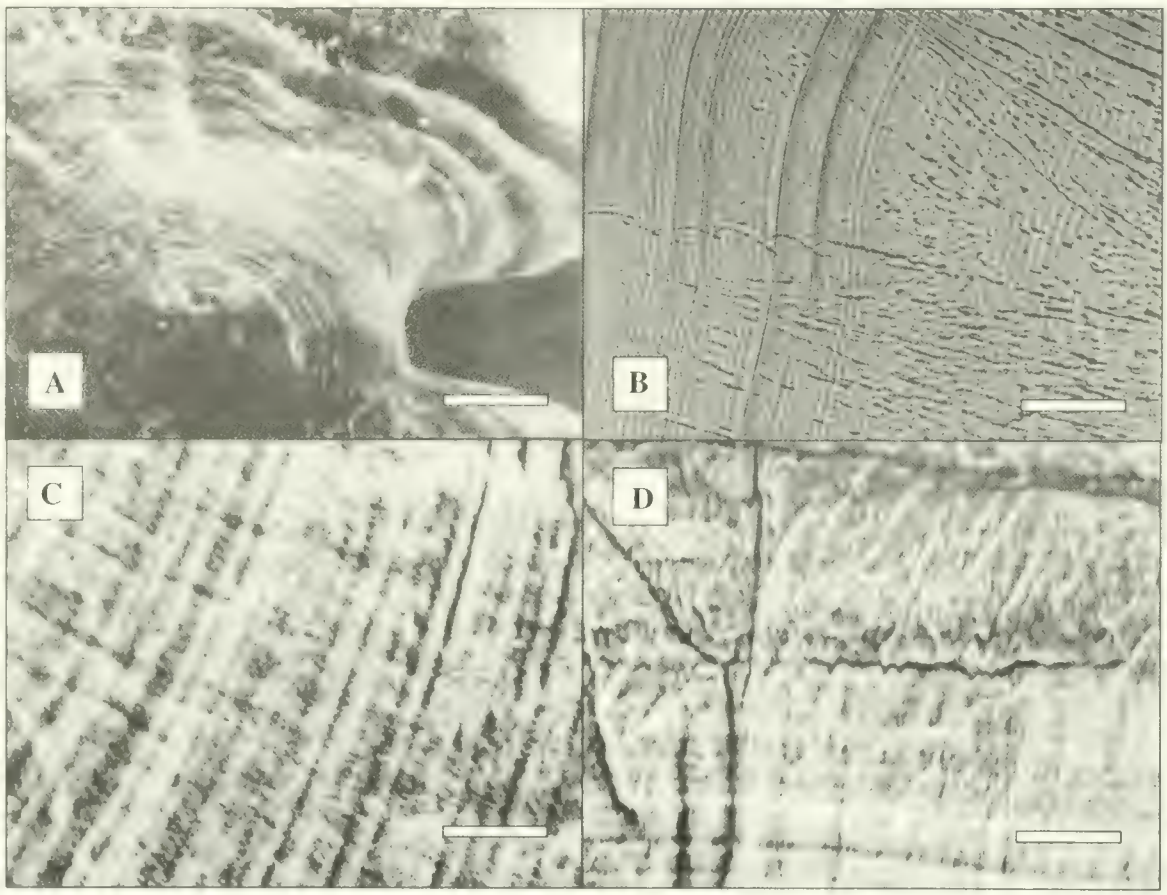

Figure 2

Scanning electron micrographs of *Coryphaena hippurus* sagittal otoliths. (**A**) Ridges on the surface of the central area of the otolith (scale bar=155 μm); (**B**) thin increments laid down in the central region of the otolith, showing rhythmic growth patterns of 7- and 14-increment groupings (scale bar=35 μm); (**C**) wider increments laid down in the outer region of the otolith (scale bar=10 μm); (**D**) rhythmic growth pattern of 14 daily growth increments (scale bar=15 μm).

n=1) to 20.6–23.9 mm (at day 36, n=3). In general, poorly defined concentric increments, consisting of an adjacent dark and a light zone, were laid down around the core (Fig. 1E). In relation between age in days and number of increments, neither the x-axis intercept nor the slope were significantly different from 0 and 1, respectively (t-test; $P>0.05$): $y = 0.3894 + 0.9846x$ (n=75, r=0.98).

From the juvenile fish, 125 otoliths were read (71%), 73 females between 19.5 and 58.5 cm FL and 52 males between 16.5 and 58 cm FL. Observed minimum and maximum ages were 47 and 176 daily growth increments. Of 36 adult fish otoliths studied with the light microscope, only 15 (42%) were able to be interpreted. A high percentage were rejected owing to error in reading precision greater than 5% or to erosion of the marginal zone during the polishing process. In specimens between 67 and 117 cm FL, the minimum and maximum ages read were 189 and 362 daily growth increments, respectively.

Scales from 139 adult specimens, measuring 65–124 cm FL, could be interpreted (93%). The results showed the presence of three age groups within the population: 67 1-yr-old specimens ranging from 65 to 110 cm FL ($\bar{x}$=87.95, SD=10.15), 61 2-yr-olds measuring 73–120 cm FL ($\bar{x}$=97.54, SD=10.95) and 11 3-yr-olds measuring 92–124 cm FL ($\bar{x}$=108.73, SD=10.17).

The von Bertalanffy growth function was calculated on the basis of the age–length relationships from daily growth rings in juvenile otoliths and annulae in adult scales (Fig. 4). Adult daily ages were not taken into account in these calculations because of observed underestimations in aging adults from

otoliths. Growth parameters for the whole population and by sex are shown in Table 2.

Length-frequency distributions for the 1990 and 1991 fishing seasons, based upon sampling of a fishery on juveniles, are given in Figure 5. Fish caught in this fishery from August to December measured 18–70 cm FL. The monthly length distribution indicated a rapid increase in the mode, mean, and minimum and maximum sizes for the catch. Von Bertalanffy growth parameters for this fraction of the population were estimated for the 1990 and 1991 fishing seasons (Table 2).

Discussion

The length–weight relationships obtained, showing negative allometric growth in females and isometry in males, are in accordance with the sexual dimorphism of *C. hippurus*. In this species there is a characteristic bullhead in males which, in the western Mediterranean, begins its development in individuals around 50 cm FL (Massutí and Morales-Nin, 1997). Similar results are obtained in other areas (Palko et al., 1982; Chatterji and Ansari, 1985), with a negative allometry that is stronger in females than in males.

Our study confirmed the daily nature of otolith growth increments in the first month of life for *C. hippurus* as reared fish. The strong correlation of mean sagittal counts to known fish age validated the use of otolith growth increments in the aging of juveniles up to 40 days old. Because regular incremental formation began on day one, no adjustment was required to estimate age from incremental counts of sagittae from wild fish.

Results suggest that the age of adult specimens is underestimated by the otolith method. This is clear when age–length relationships from daily growth rings in otoliths and from annuli in scales are plotted. For the same size interval, the otolith reading gave ages between 0 and 1 year, whereas interpretation of annuli in scales of adult fish gave ages to 3 years. This might be due to methodological problems in otolith preparation and interpretation. Consequently, the use of scales seems to be the best aging method for adult fish from the Mediterranean, from the point of view both of preparation and of results obtained.

The interpretation of juvenile fish age from daily growth increments seemed accurate, with a low percentage of disagreement between readers. To test the precision of this method, juvenile birthdate distribution was calculated by subtracting age in days from the date of capture. This showed a long period with peaks in the second fortnight of June 1990 and the first fortnight of July 1991 (Fig. 6). This small variation between years might be due to changes in the spawning peak or to differential mortality (Campana

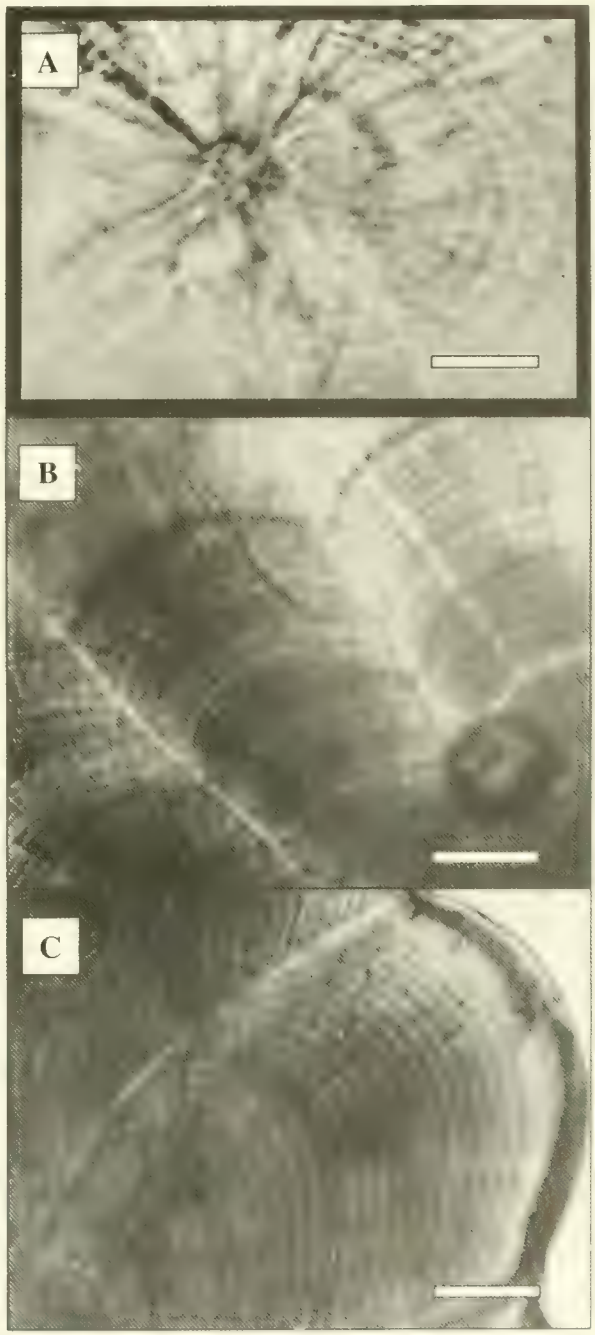

Figure 3

Light micrographs of *Coryphaena hippurus* sagittal otoliths. (**A**) Daily growth increments in the core region of the otolith (scale bar=15 μm); (**B**) narrow increments in the central region of the otolith, showing rhythmic growth patterns of 7-, 14-, and 28- increment groupings (scale bar=25 μm); (**C**) wider increments in the area of the otolith edge (scale bar=30 μm).

Table 2

Von Bertalanffy growth parameters for *Coryphaena hippurus* calculated by different methods. The standard errors of each parameter are in parentheses. n = number of specimens; L_∞ = asymptotic length (cm FL); k = growth coefficient in 1/yr; Rn = goodness-of-fit index; r = correlation coefficient; Φ = growth performance index. LFA is length-frequency analysis; S and O are scale and otolith readings.

Population	Sample	Method	n	L_∞	k	t_0	Rn	r	Φ
Juveniles	1990	LFA	2635	72.4	2.5	—	0.447	—	4.118
Juveniles	1991	LFA	1449	74.8	2.5	—	0.304	—	4.146
Females	1990–91	S and O	132	110 (2.62)	1.56 (0.14)	0.008 (0.02)	—	0.92	4.277
Males	1990–91	S and O	132	98.7 (1.59)	2.06 (0.19)	0.024 (0.02)	—	0.91	4.302
Whole	1990–91	S and O	264	102.4 (1.56)	1.90 (0.15)	0.023 (0.02)	—	0.87	4.300

and Jones, 1992). According to our results and those of Uchiyama et al. (1986), the deposition of increments in otoliths begins on the first day of life. In addition, ripe eggs hatch within 50–60 hours after fertilization, depending on temperature (Palko et al., 1982). Thus, hatching distribution can be compared with the spawning period of the species in the area, which is known from adult fish maturity data (Massutí and Morales-Nin, 1995, 1997). The agreement between these hatching dates and the above-mentioned data supports the daily ages determined from otoliths of wild juvenile fish.

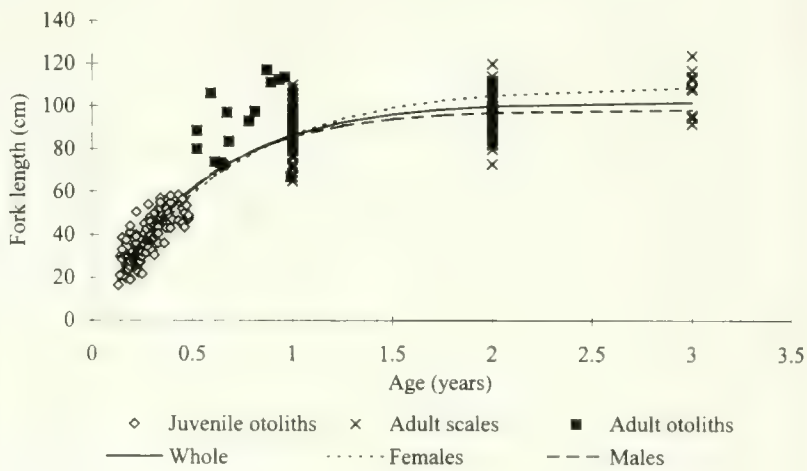

Figure 4

Age–length relationships and von Bertalanffy growth curves obtained from scale and otolith interpretation in *Coryphaena hippurus* adults and juveniles.

Another independent verification method uses link frequency analysis. The modal progression in juvenile catches showed a rapid growth rate, which is reflected by the almost double increase in monthly mean length during the fishing season from late August to early December. This rapid growth is in accordance with results obtained in the Mediterranean and other areas with reared specimens (e.g. Hassler and Hogarth, 1977; Reñones et al., 1992; Ayari et al., 1995; Benetti et al., 1995b), and with the estimates of growth rates between 3 and 10 cm per month, obtained from modal progression analysis on wild specimens in different areas (Wang, 1979; Oxenford and Hunte, 1983; Murray, 1985).

Growth parameters obtained by the two different methods used for the two population groups were quite different owing to the different length ranges considered. Nevertheless, similar results are obtained with the growth performance index. These values are similar to those calculated from growth parameters reported from scales of annuli by Beardsley (1967) and Rose and Hassler (1968), which were 4.27 and 4.19, respectively. Those calculated from growth parameters obtained by daily growth increments (Uchiyama et al., 1986) were slightly higher (4.52 for females and 4.63 for males), probably owing to the above-mentioned underestimation of age in adult fish with this method, the few adult specimens studied, and the effect of temperature on growth and metabolism. Temperatures can also explain the slower growth rate of *C. hippurus* in the western

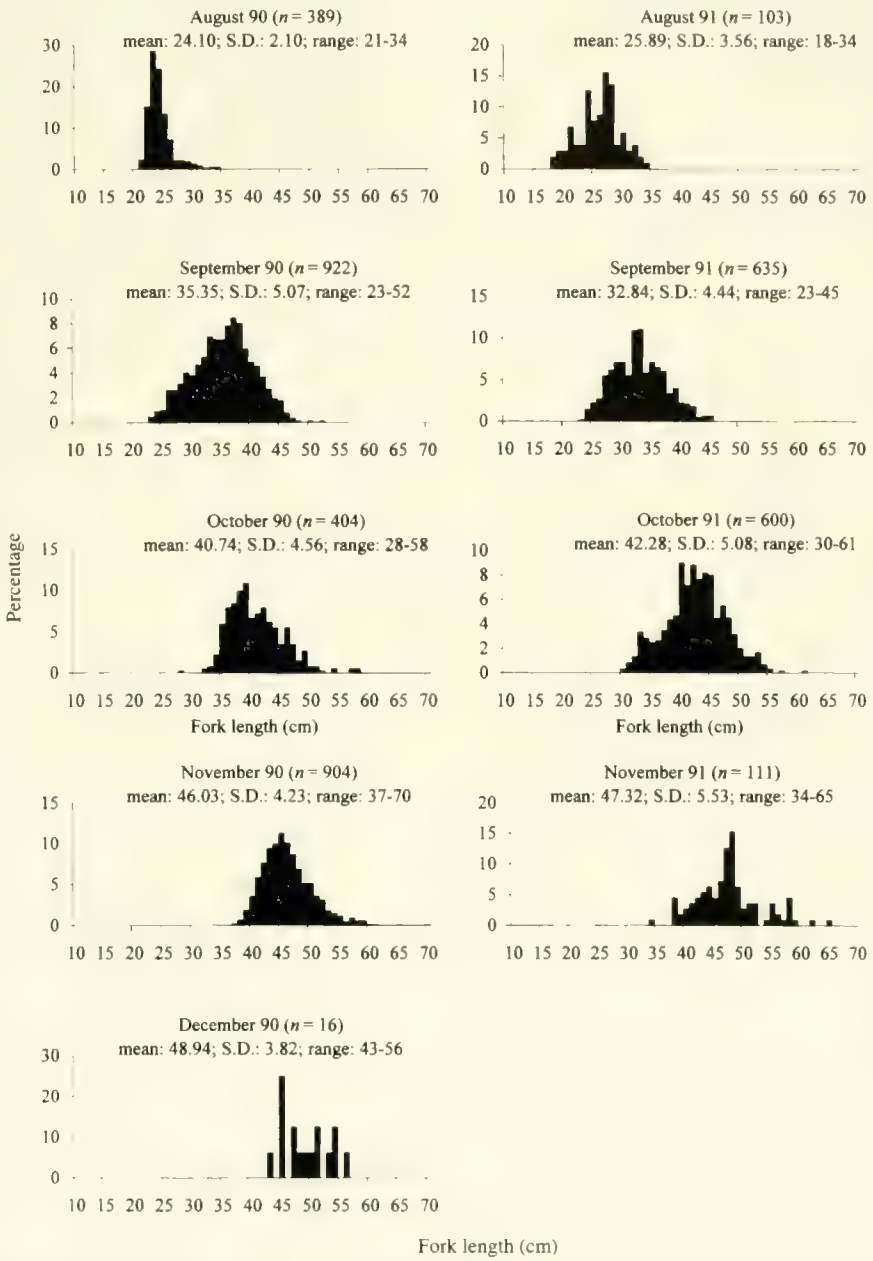

Figure 5

Monthly length–frequency distributions of juvenile *Coryphaena hippurus* caught off Majorca with the surrounding net during the 1990 and 1991 fishing seasons. Fork length in cm (*n*=number of specimens; SD=standard deviation).

North Atlantic Ocean (Beardsley, 1967; Rose and Hassler, 1968), where a decreased feeding rate when water temperature falls below 23°C and a cessation of feeding at 18°C have been reported (Hassler and Hogarth, 1977). By contrast, in Hawaiian waters, where faster growth rates have been reported, this species feeds throughout the year and can be expected to grow continuously (Uchiyama et al., 1986).

The growth-rate values obtained for *C. hippurus* are within the range reported from otolith microstructures by Brothers et al. (1983) for Atlantic bluefin tuna (*Thunnus thynnus*), another top-level predator characteristic of the western Mediterranean epipelagic ecosystem. According to Benetti et al. (1995a), *C. hippurus*, Scombridae species, and *Isurus oxyrhinchus*, another Mediterranean pelagic predator, have common factors

in environment and lifestyle which must strongly select for anatomical, biochemical, and physiological adaptations necessary to achieve exceptionally high metabolic rates. Such selection leads to high somatic and gonadal growth rates, rapid digestion, and quick repayment of oxygen debts, all important functions in these active pelagic predators.

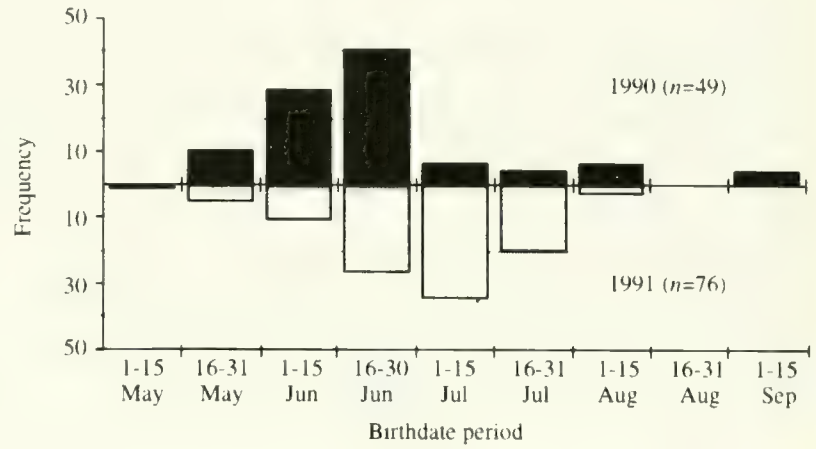

Figure 6

Frequency distribution of back-calculated birthdates for *Coryphaena hippurus* juvenile specimens in 1990 and 1991.

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Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska

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Abstract.—The social structure and genealogical relationships of resident killer whale pods in Prince William Sound, Alaska, are inferred from association analysis and direct observation. During 1984–95 a total of 2444 hours of observation were made and 36,009 photographs were taken of identifiable killer whales. Cole's association index and a point correlation coefficient index were used to test the statistical significance and strength of associations between individuals, and a clustering procedure was used to delineate group structure. A total of 202 whales were grouped into 9 pods. Genealogical relationships were inferred from the strength of bonds among pod members. Genealogical trees suggested that intrapod groups were matrilineal in structure. Splitting of one pod (AN pod) was observed during the study; however, there was no splitting of matrilineal groups.

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It is well established that individual killer whales can be recognized by unique marks, scars, and pigmentation patterns (Bigg et al., 1987; Heise et al., 1992). During the past 25 years a number of studies have used this fact to investigate the life history, behavior, population dynamics, vocalizations, abundance, and movements of killer whales in coastal waters of the eastern North Pacific including Prince William Sound, Alaska (Balcomb et al., 1982; Bigg et al., 1990; Olesiuk et al., 1990; Ford, 1991; Matkin et al., 1994). As a result of these studies, at least two forms of killer whale, termed "resident" (fish-eating) and "transient" (mammal-eating), have been described in the nearshore waters of Puget Sound, British Columbia, and southern Alaska (Bigg, 1982; Leatherwood et al., 1990; Morton, 1990; Ford et al., 1998; Saulitis et al., in press). Although resident and transient killer whales occur sympatrically, they are considered separate populations owing to genetic variation in mtDNA haplotypes (Stevens et al., 1989; Hoezel and Dover, 1991) and microsatellite variation in nuclear DNA (Hoezel et al., 1998). Mating between the two forms has not been observed and resident and transient killer whales have not been seen traveling together (Morton, 1990; Saulitis, 1993; Matkin et al., 1994). Studies in British Columbia and Washington indicate that resident whales of both sexes remain in their natal pods for life, whereas transients appear to have a more fluid social structure (Bigg et al., 1990).

The social organization of resident killer whales in Prince William Sound has been previously described from direct observation of associations among individuals (Leatherwood et al., 1984; Heise et al., 1992). These studies name pods on the basis of observation of groups of individuals that repeatedly traveled together. Each identifiable whale is assigned an alphanumeric code (Leatherwood et al., 1984;

Ellis, 1987; Heise et al., 1992). The first letter in the code (A) designates Alaska, followed by a letter (A–Z) indicating the animal's pod as determined by observational data. Individuals within a pod are assigned sequential two-digit numbers. Pods that result from an observed splitting of a pod share letter designations, i.e. AN10 and AN20 pod.

In this study, we tested the hypothesis that Prince William Sound resident killer whales form nonrandom associations by examining the structure of some of the extensively studied pods in greater detail. Bond strength was established by direct observation of the proximity of whales to one another and by statistical analysis of the association of individuals in photographic sequences. We used statistical analyses to evaluate whether association patterns were random and used clustering techniques to describe underlying association patterns. Subsequently, we inferred genealogical relationships as an explanation for observed association patterns.

An understanding of social organization and genealogy is a prerequisite for studies of the sociology, life history, and population dynamics of Prince William Sound resident killer whales.

Materials and methods

Field methods

Field observations and photographs used in this analysis were collected from 1984 to 1995 in Prince William Sound, Alaska, and adjacent waters. Data were obtained throughout the Sound, although the study was centered in the southwestern portion. Field work occurred from April to October, but the greatest effort and the majority of encounters with resident pods occurred in July, August, and September. Vessels used to approach the whales to obtain photographs ranged in length from 4 to 9 m and in power from 50 hp outboard motors to 185 hp diesel inboard–outboard engines.

The techniques used to approach and photograph individuals were consistent over the duration of the study. During each encounter, individual whales were typically photographed several times from a distance of 15–30 m. Individual photographs were taken of the left side of each whale, showing details of the dorsal fin and gray saddle patch, with the technique developed by Bigg et al. (1986). An effort was made to move systematically through the pod and to obtain lateral-aspect photographs of individuals, such that each filled at least 50% of the frame. Photographs were taken during all behavioral modes and when whales were tightly grouped (i.e. resting) as well as when they were spread over a considerable distance (i.e. feeding). Encounters lasted until all whales were photographed or until weather or darkness (or both) made photography impracticable.

In the early years of the study we used a 35-mm SLR Nikon FM2 camera with an autowinder mounted on a shoulder brace. Later this setup was replaced by a 35-mm SLR Nikon 8008 autofocus camera with a shoulder brace. In all years a 300-mm lens was used and Ilford HP5 35-mm film was exposed and processed at ISO 1600.

Data recorded during each encounter with killer whales included date, time, duration, and location of the encounter. The total number of individuals present, the identity of individuals that could be immediately recognized, and the general behavior of the whales (i.e. feeding, resting, traveling, socializing, and milling) were also noted. Whales were considered associated on the basis of direct observation when they were seen traveling in the same direction and at the same speed for a period of greater than a few minutes and for a distance less than several body lengths.

Analysis of photographs

Throughout the study, each photographic frame was examined numerous times with a dissecting microscope to insure that all individuals were correctly identified (Bigg et al., 1987). Mothers of new calves were identified on the basis of consistent close association of calves with a specific female (Bigg et al., 1990). Identified individuals were recorded in a standard format to facilitate computer analyses, and uncertain identifications were excluded from the analysis.

Data analysis

In order to test the hypothesis that killer whales form nonrandom associations, associations between individuals were examined by using statistical analysis of photographic data. Photographs were placed in the order in which they were taken, and the identity of all individuals in each frame was tallied for each encounter. The analytical program examined associations between animals within photographic frames and in immediately adjacent frames. Photographic sequences that contained less than two individuals were deleted because they provided no information on association among individuals. Data from the remaining frames were accumulated in a 2×2 contingency table for each pair of whales for all years in which both individuals were photographed:

		First whale		
		Present	Absent	Total
Second whale	present	a	b	$a+b$
	absent	c	d	$c+d$
	total	$a+c$	$b+d$	n

where $(a + c)$ and $(a + b)$ denote the total number of occurrences of the first and second individuals respectively, a the number of joint occurrences, and d the total number of frames in which neither whale occurred in years in which both were photographed.

First, the degree of association between all individuals was measured by using Cole's (1949) association index (CAI):

$$CAI = \frac{ad - bc}{(a+b)(b+d)} \quad \text{for } ad > bc,$$

$$SE = \frac{(a+c)(c+d)}{n(a+b)(b+d)}$$

$$CAI \quad \frac{ad - bc}{(a+b)(a+c)} \quad \text{for } bc > ad \text{ and } d > a,$$

$$SE = \frac{(b+d)(c+d)}{n(a+b)(a+c)}$$

$$CAI \quad \frac{ad - bc}{(b+d)(c+d)} \quad \text{for } bc > ad \text{ and } a > d,$$

$$SE = \frac{(a+b)(a+c)}{n(b+d)(c+a)}.$$

The index was expressed as a percentage ranging from 100 to –100, with 100% indicating that the joint number of occurrences of each whale equaled the number of occurrences of the least-photographed individual. Zero percent indicated that the individuals were randomly distributed among photographs, and –100% indicated that the two individuals were never photographed together. The statistical significance of CAI values was evaluated according to their standard errors using Student's t test (Cole, 1949).

The CAI provides a measure of complete association (rather than absolute association) in that a value of 100% occurs only when the joint number of occurrences equals the number of occurrences of the less frequently photographed individual (see Cole, 1949, for details and a review of association indices). An index of complete association was deemed more appropriate for an analysis of patterns of association between individuals because not all individuals were equally identifiable (see Bigg et al., 1990) as was especially the case for cow–calf pairs, in which the often well-marked mother was generally identified in more photographs than her usually indistinct young calves even though they always traveled together.

Only CAI values for all years' combined were used to determine intrapod groups. CAI values were later calculated for the periods 1984–88 and 1989–95 and used to examine changes in bond strength between mothers and female offspring as the offspring matured and produced their own calves. The relationship between age of males and the bond strength with their mothers was also examined with these CAI values.

Groupings of individuals were identified from dendrograms constructed with an agglomerative average single-link algorithm (Johnson, 1967; see Fig. 1) In this procedure, CAI values for all possible pairs of individuals were compared and the pair with the highest CAI was linked. Then the pair of unlinked individuals with the highest CAI was linked, or an unlinked individual with a higher mean CAI value with previously linked individuals was linked to that pair, and so on until the mean CAI dropped to 20%. By this point, the vast majority of individuals had been linked into intrapod groups and we switched to an analysis with the point correlation coefficient (PCC):

$$PCC = \frac{ad - bc}{\sqrt{[(a+b)(a+c)(b+d)(c+d)]}},$$

where a represents the number of photographs containing one or more members of both groups, b and c represent the numbers containing members of only one or the other of the groups, and d represents the number containing no members of either group.

The PCC index, a measure of absolute association, was used to examine associations among intrapod groups determined by CAI analysis because each group was considered equally identifiable. The PCC index varies from 100% to –100%, with 0 indicating a random distribution. An index of absolute association was deemed to be more appropriate for intrapod groups because all groups contained readily identifiable animals; therefore observation of one group in the absence of another group indicated that each group was traveling independently of one another. The relationships among intrapod groups were examined from dendrograms constructed from PCC values with an agglomerative average single-link algorithm (see Fig. 2). Linkages with a positive PCC

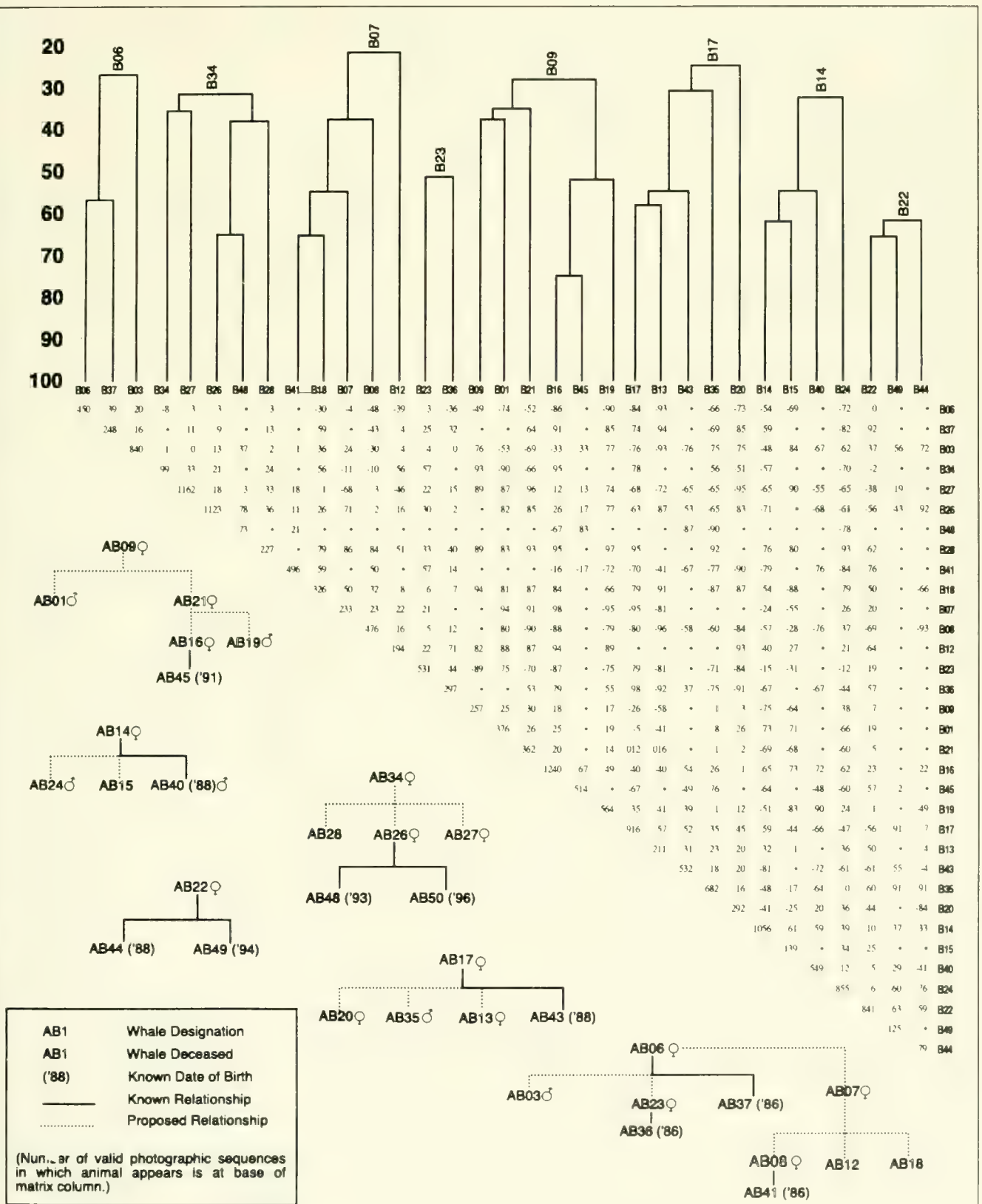

Figure 1

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups are shown in Fig. 2.) Middle: matrix of CAI values between pairs of individuals calculated at the pod level for AB pod, AB17 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

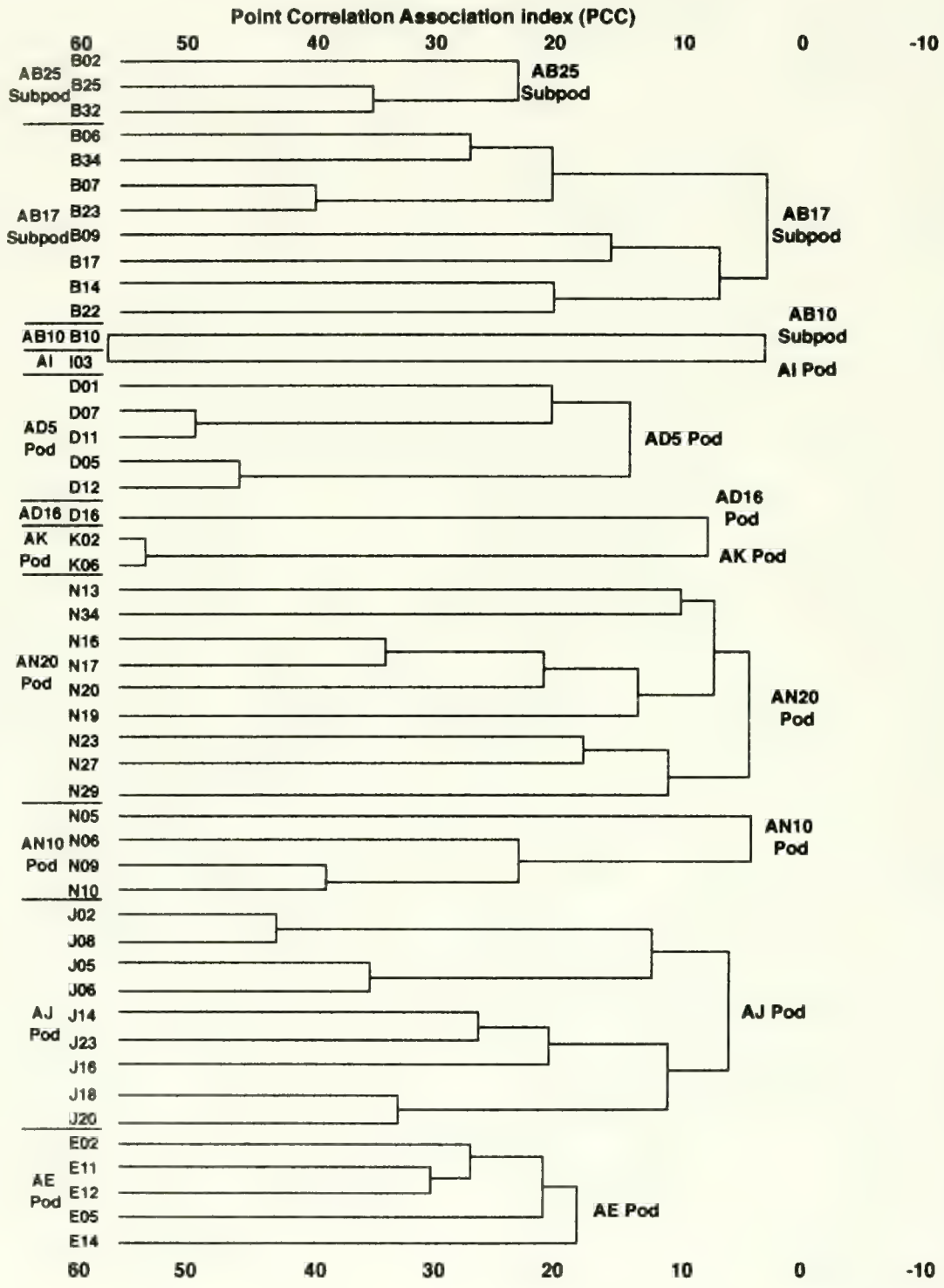

Figure 2

Dendrogram illustrating the relationships among intrapod groups (see top of Fig. 1 and Figs. 3–12) with values derived from PCC analysis.

association value (PCC>0) were designated as pods (Fig. 2). Groups were designated as subpods rather than pods when PCC values between them did not exceed zero but direct observation and photographic

summaries of encounters indicated that designated subpods traveled together as a single pod over 50% of the time.

Determination of sex and age

Sexually mature males were differentiated from females and immature males by their higher dorsal-fin height-to-width ratio (HWR), which typically exceeds 1.4 by 15 years of age (Olesiuk et al., 1990). Mature females were identified when they gave birth and were accompanied by a new calf. The sex of most juveniles could not be determined except in cases where the penis or the unique pigmentation pattern of the genital region was observed (Bigg et al., 1990; Olesiuk et al., 1990).

Actual ages could be determined for whales born during the study on the basis of their birth year. The ages of whales that were immature at the beginning of the study were estimated when they were first seen on the basis of relative size of the whale and size of the dorsal fin (Bigg et al., 1990). The approximate year of birth for whales that matured during the study was estimated by subtracting the mean age of maturity (15 years for both sexes) from the year they matured. Females were considered to have matured in the year they gave birth to their first viable calf, and males in the year in which their dorsal fin attained an HWR of 1.4 (Bigg et al., 1990; Olesiuk et al., 1990). The year of birth of males that were sexually but not physically mature at the start of the study was estimated by subtracting the mean age of physical maturity from the year their dorsal fin attained a HWR of 1.6–1.8, indicating physical maturity. Males that were physically mature and had a dorsal fin HWR of 1.6–1.8 at the beginning of the study were considered to be at least 21 years of age at that time. The minimum age of females that were mature at the beginning of the study was estimated by subtracting 15 years from the estimated birth year of their eldest offspring. This was a minimum estimate because a female's elder offspring may have died before the start of the study. Females that had not given birth for a decade or more were considered postreproductive (Olesiuk et al., 1990).

Construction of genealogical trees

Because statistical analysis indicated that whales associated in stable groups (or pods), CAI values were recalculated for all individuals within each pod and displayed in a matrix to show the relative strength of association among pod members (Fig. 1). We postulated that associations within pods reflected genealogical relationships and used them in conjunction with data on known relationships, sex and age data, and direct observations to infer genealogical relationships (Fig. 1).

Possible maternal genealogical trees were constructed in three steps (Bigg et al., 1990). Individuals to be incorporated into the tree as offspring were selected beginning with those born during the study, followed by those that were juvenile at the start of the study, and finally by those that were mature at the start of the study. Second, their potential mothers were identified. All mature females in the same pod were considered, providing that they could have been at least 12 years (minimum age of maturity) older. An individual's own mature daughters were excluded as potential mothers. Third, the relative strength of bonds as indicated by CAI values between the individual and all its potential mothers was examined. The potential mother with which the individual was most closely bonded was assumed to be its mother. An individual not strongly bonded to any potential mother was not assigned a mother. Matrices were cross-checked to insure that mother–offspring assignments created sibling groups that demonstrated reasonable linkage by CAI values. Direct observation was used to supplement statistical analysis to construct genealogies in instances where individuals and groups were less frequently photographed and where there was some ambiguity in the numerical analysis.

Results

A total of 2444 hours of direct observation of whales was logged from 1984 to 1995 (Table 1), during which 36,009 frames of film were exposed that were suitable for use in statistical analysis of association patterns (more than one individual appeared in the photographic sequence). A total of 202 whales photographed between 1984 and 1995 were included in the association analysis. According to direct field observations and inspection of photographs, these had previously been assigned to 9 pods (Table 2; Heise et al., 1992). Another 158 whales were tentatively grouped into 5 pods by field observation and visual inspection of photographs (pod AX, 54 whales; pod AY, 11 whales; pod AS, 17 whales; pod AF, 48 whales; pod AG, 28 whales). These pods were not included in the association analysis because there were insufficient photographs. The individuals listed in Table 2 represent the cumulative membership of pods over all years of the study. In all pods and most groups, the numbers of individuals varied over the course of the study as members died or were born during the study.

Table 1
Hours of direct observation and number of usable film frames by year.

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Frames	6,076	1,284	2,967	1,326	1,400	3,549	5,940	3,701	3,641	2,333	1,662	2,130	36,009
Hours	307	154	127	91	92	268	423	246	255	127	120	234	2444

Statistical analysis indicated that individual whales did not associate randomly with one another. For individuals seen together at least once, 38.5% of all CAI values from the initial analysis of all individuals in all years were significantly less than 0 at a 5% confidence level (30.1% at a 1% level) and 27.5% were significantly greater than 0 at a 5% level (23.2% at a 1% level) (see Cole, 1949). Because these values are far greater than expected owing to chance, we rejected the null hypothesis that association patterns were random. The various animals positively associated with a particular individual tended to be positively associated themselves. These groups were also indicated by the agglomerative cluster analysis. A dendrogram showing associations among all 202 individuals included in the analyses was too large to exhibit here as a single figure; it appears split into pods along with matrices of CAI values and proposed genealogical trees for each pod (Figs. 1, and 3–12)

Table 2
Pods and individual whales used in this analysis.

Pod	Cumulative membership
AB	AB01-AB51
AI	AI01-AI07
AJ	AJ01-AJ38
AE	AE01-AE20
AK	AK01-AK14
AN10	AN01-AN03, AN05-AN12, AN35,AN38, AN40-AN41, AN45-AN51
AN20	AN04, AN13-AN34, AN36-AN37, AN39, AN42-AN44
AD05	AD01-AD12, AD19,AD21-AD27
AD16	AD13-18, AD20

In nearly all cases, intrapod groups of individuals linked by association analysis at greater than 20% CAI reflected groupings established by direct observation. Direct observation also indicated that these intrapod groups virtually always traveled together. Most intrapod groups were centered around a reproductive or postreproductive female, which led us to suspect that these groups reflected matrilineal genealogies. However, in four cases single males (AE14, J02, N19, and D01) were not joined to other intrapod groups (CAI>20%) and in two cases pairs of males (AD02 and AD12, and AB02 and AB29) were linked to each other but not to other intrapod groups (CAI>20%). The nine pods examined contained 48 intrapod groups, including male singles and pairs (Figs. 1 and 3–12). With the exception of AB pod, pods comprised 1–9 intrapod groups. Two pods (AI and AD16) contained only one intrapod group. The three subpods of AB pod contained a total of 12 intrapod groups. Intrapod groups were composed of 1–9 individuals.

Patterns of association between intrapod groups, as indicated by statistical analysis, generally supported the pods constructed by direct observation. Forty-six of the 48 intrapod groups (190 of 202 individuals) were linked at the zero level of association into their respective pods (Fig. 2). There were two exceptions; repeated direct observations were used to clarify separations into intrapod groups. First, the AB10 subpod was linked in the dendrogram with AI pod (PCC=4) before it was linked with the other subpods of AB pod. Second, AK pod and AD16 pod formed distinct clusters as expected but were joined at the PCC = 8 level, which was greater than the zero level adopted to define the other pods.

On the basis of direct observation, AN10 pod and AN20 pod were considered a single pod (AN pod) until 1989, when they began traveling separately a majority of the time. AN whales were encountered on 46 occasions during 1984–88; the AN10 and AN20 groups were observed together in 35 (76%) of these encounters. In contrast, during 1989–95 they were observed together in only 3 of 65 (5%) encounters where AN whales were present. After 1992 they were not seen traveling together and were thus designated as separate pods. The association analysis supported their designation as separate pods (Fig. 1). AD pod was also considered a single pod early in the study on the basis of direct observation during a few encounters. From more recent direct observation and the results of the association analysis, it is now designated as two pods (AD5 and AD16 pods).

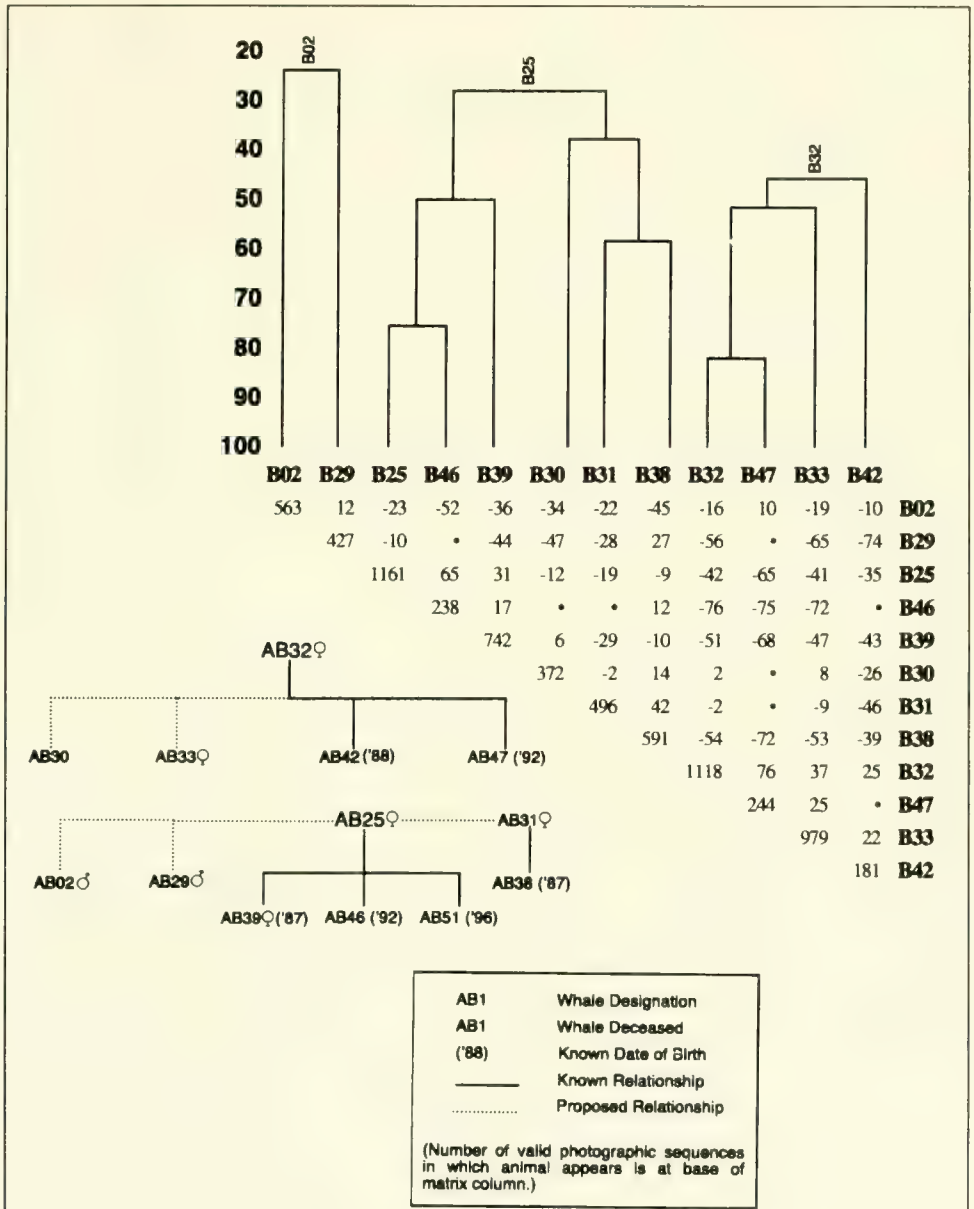

Figure 3

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB25 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

On the basis of lack of linkage in the PCC dendrograms above the zero level, AB pod was divided into three subpods (AB10, AB17, AB25), although prior to 1994, direct field observations indicated that these subpods very rarely traveled separately. However, even when traveling together, the subpods typically traveled as cohesive units within the pod. Since 1994, direct observation has indicated that the AB25 subpod has split off and travels mainly with AJ pod. Other than those established for AB pod, no other subpods were identified in the study.

To explain association patterns within intrapod groups, we postulated that these represented matrilineal groups and that genealogical relationships

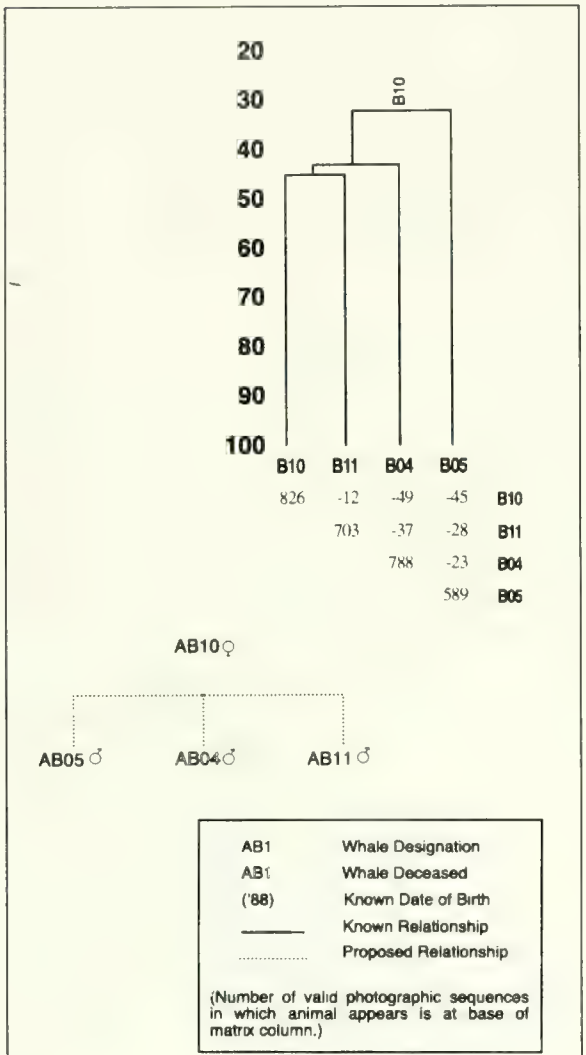

Figure 4

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 12.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB10 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

could be deduced by examination of bond strengths within these groups. CAI values were calculated between all individuals of each pod and dendrograms of the CAI values were constructed to reveal the structure of associations between the members of each pod (Figs. 1, and 3–12).

The individuals in the nine pods examined in the second CAI analysis were placed in 39 postulated

Table 3

Cole's association index (CAI) values for mothers and female offspring that produced their first calf in 1987 or later.

Reproductive offspring	Year of first calf	Mother	CAI 1984–1988	CAI 1989–1995
AJ3	1990	AJ8	28	13
AJ4	1994	AJ8	57	20
AJ13	1992	AJ14	40	33
AK7	1993	AK6	51	24
AN10	1987	AN9	22	-20
AN11	1992	AN9	30	23
AN26	1990	AN23	53	34
AN31	1990	AN20	28	19
AN35	1988	AN9	29	2

maternal genealogical trees on the basis of linkages established in association analysis. An additional four newborn calves were observed in 1996 and placed in the genealogical trees on the basis of field observations only. Genealogical trees were constructed by first establishing all known mother–offspring relationships from field observations. There were 58 offspring born during the study that appeared in the photographs used for association analysis. In all but one case (AB41 and mother AB8), the CAI values between offspring and their known mothers was higher than for any other pairings of individuals. Direct observation also indicated that offspring maintained their strongest bonds with their known mothers throughout the study period. The three offspring born at the beginning of the study were still most strongly bonded to their mothers after 12 years. These were mother–offspring pairs AI3 and AI4 (CAI=27); AK6 and AK8 (CAI=34); and AE11 and AE13 (CAI=46).

The strength of the bond between females and their mothers declined in the nine cases in which females became reproductive during the study and their mothers remained alive throughout the study (Table 3). A paired t test of CAI values for 1984–88 and CAI values for 1989–95 showed that the tendency for associations to decline after female offspring become reproductive was statistically significant (t=4.88, P=0.0012).

There were 31 juveniles (estimated age 10 years or less in 1984) at the beginning of the study. Association analysis indicated that all but five of these whales remained most closely bonded to the whales judged by direct observation to be their mothers. Three of these exceptions were females that produced calves (AK7 and calf AK12; AN8 and calves AN41

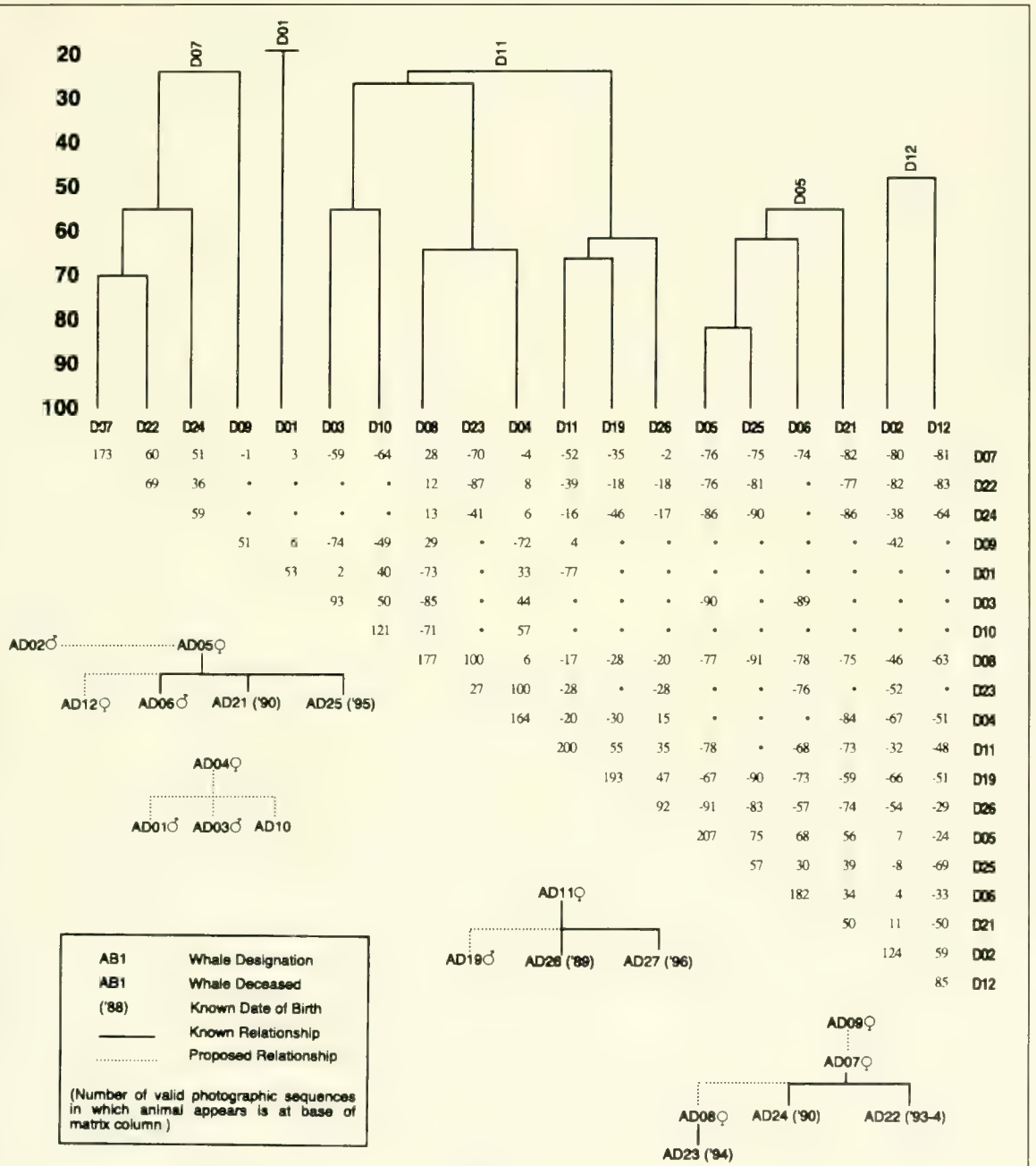

Figure 5

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD5 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

and AN48; AN11 and calves AN47 and AN49). These females became most closely bonded to their own calves rather than to their mothers. One juvenile male, AN19, had a stronger bond with apparent juvenile sibling AN18 (CAI=16) than with his apparent mother, reproductive female AN17 (CAI=4). The juvenile AB18 had a stronger bond (CAI=58) with a young calf, AB41, in his intrapod group than with his apparent mother, reproductive female AB7 (CAI=22). However, in the cases of all five of these whales, the strongest bond with an adult female remained with their apparent mothers.

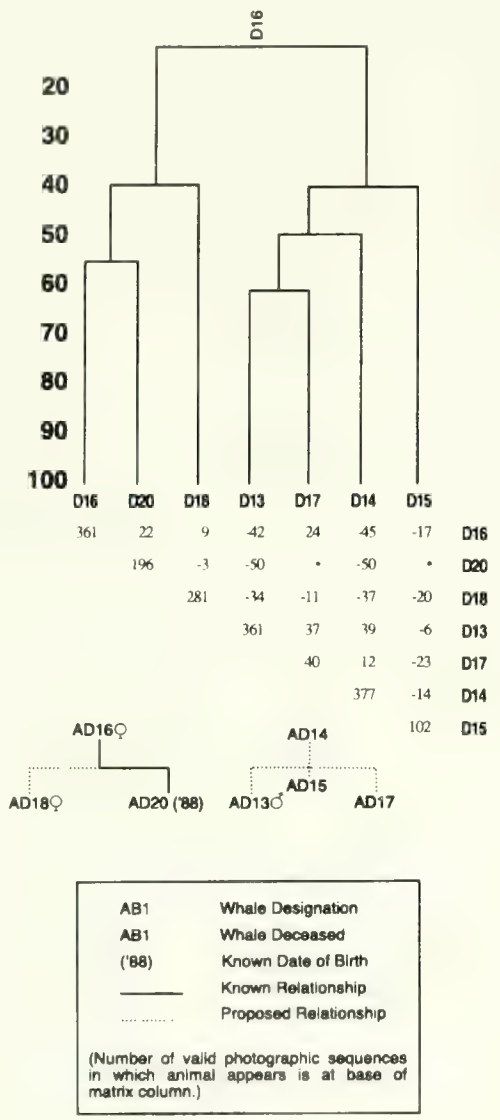

Figure 6

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD16 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

The strength of bonds between male offspring and their mothers was highly variable (Table 4). Simple regression analysis indicated that the strength of bonds tended to diminish with age, but not significantly ($F_{1,27}$=1.62; P=0.215).

Table 4

Cole's Association Index (CAI) values for male killer whales and their mothers. Ages estimated as described in methods; ages over 20 years are mimimum ages.

Whale	Estimated approx. age (yr)	CAI Value	Whale	Estimated approx. age (yr)	CAI Value
AB1	33	25	AJ9	18	32
AB3	30	20	AJ16	27	48
AB24	25	39	AJ17	29	18
AB35	19	35	AJ21	19	31
AJ25	22	48	AK4	27	29
AD3	27	50	AK1	27	20
AE1	32	25	AN3	32	31
AE3	18	21	AN7	24	17
AE6	16	38	AN14	19	47
AE14	19	24	AN21	25	54
AE9	32	31	AN24	15	55
AJ1	31	39	AN25	24	28
AJ2	27	21	AN30	16	54
AJ7	19	55	AN33	23	41
AN1	32	66			

Of the 45 proposed maternal lineages (Figs. 3–12), 25 included two generations, 16 included three generations, and four had four generations. In all but one of the four-generational trees, the oldest matriarch died during the study. We identified four matrilineal intrapod groups that appeared destined to die out. These were the single adult male, AB3 (Fig. 4); the AB10 subpod which consisted of the apparently postreproductive female AB10 and 3 adult male sons, AB4, AB5, and AB11 (Fig. 6); the apparently postreproductive AJ12 and her adult male son, AJ16 (Fig. 9); and the apparently postreproductive AN 34 and her adult male son, AN21 (Fig. 10). Three of the remaining matrilineal groups had produced two reproductive females in one generation and were growing, and eight had produced one reproductive female and were relatively stable. The fate of the other matrilineal groups will be determined later as offspring born during the study mature and their reproductive potential is realized.

Discussion

Direct observations indicated that resident killer whales in Prince William Sound do not associate randomly with one another, but rather tend to associate with specific individuals. Statistical analysis of associations in photographic sequences supports this

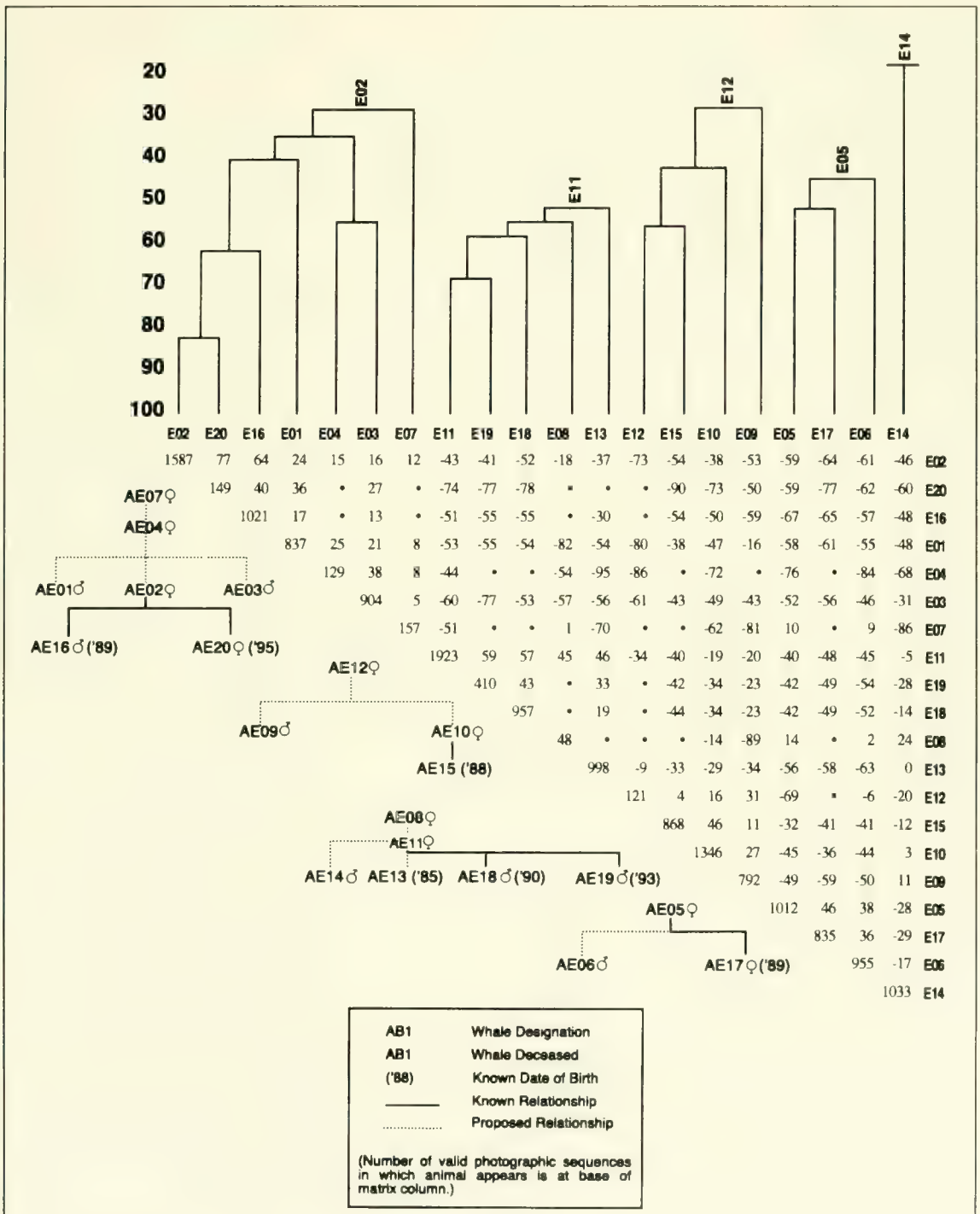

Figure 7

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AE pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

observation. It is important to appreciate that in this analysis (Fig. 1 and subsequently Figs. 3–12), results were obtained by using a continuous clustering process in which all whales were treated as individuals

and were linked into progressively larger groups until they formed a single large group. This analysis examines the relationships between individuals in the entire population.

We postulate that the significant long-term associations observed were based on genealogical relationships. Judged from known relationships (mothers and offspring born during the study), the strength of bonds among individuals within pods appeared directly correlated with their degree of relatedness.

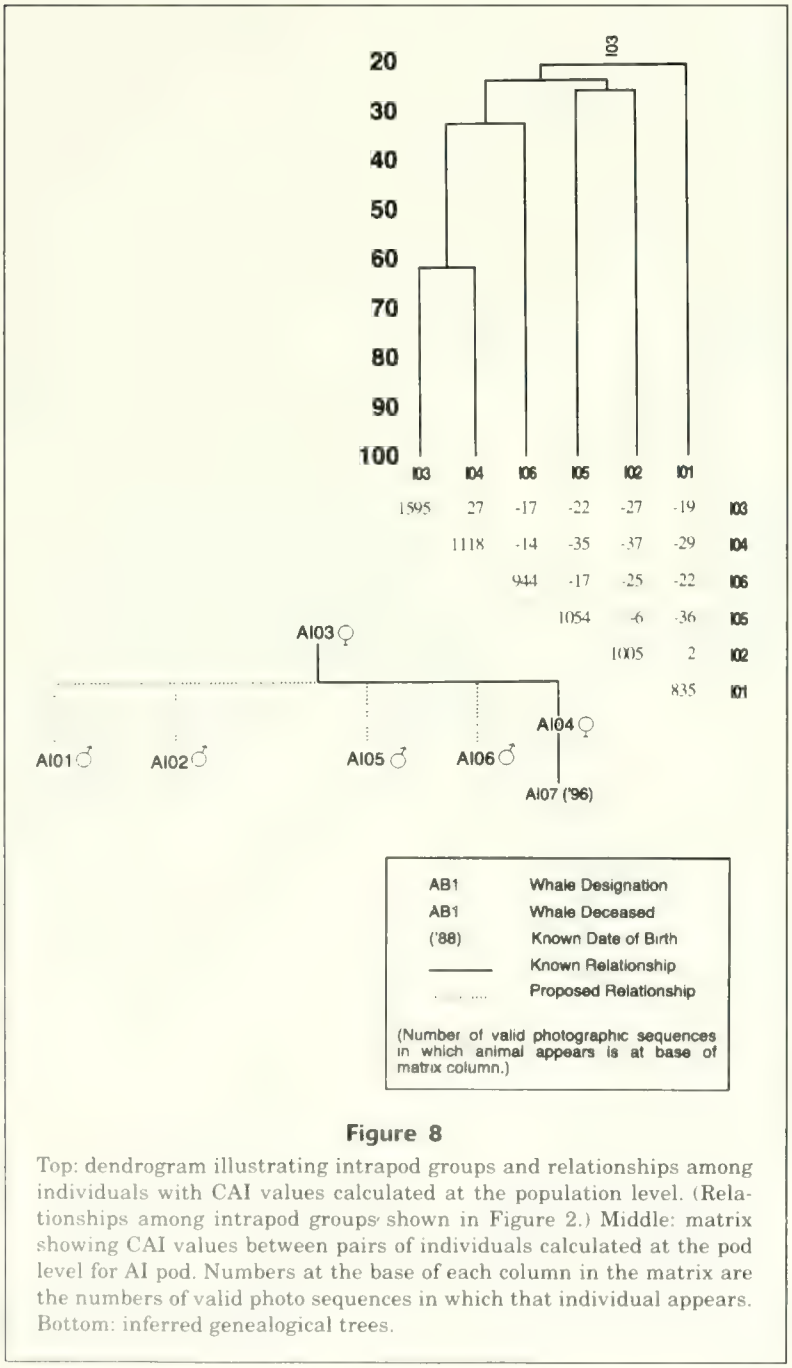

Figure 8

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Figure 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AI pod. Numbers at the base of each column in the matrix are the numbers of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

Our findings that resident killer whales in Prince William Sound are organized in statistically identifiable pods and intrapod groups are similar to results from studies of resident killer whales in British Columbia and Washington State (Heimlich-Boran, 1986; Bigg et al., 1990). Bigg et al. (1990) defined a pod as a group of individuals that traveled together at least 50% of the time. All the resident pods described in Prince William Sound fit that definition. Pod membership is also supported by pod-specific vocal dialects in both areas (Bigg et al., 1990; Ford, 1991; Ford[1]).

Pod delineations based on direct observation were supported by association analysis in all but two cases. Both discrepancies appeared in the final stages of the agglomerative linking procedure. Although each pod was a distinct cluster, AD16 pod was found to be linked to AK pod with a PCC value of eight, at somewhat higher than the level of linkage between other pods. This was not supported by direct observation and was apparently an artifact of small sample size. AD16 pod was infrequently photographed and was often part of multipod groups that included AK pod.

The AB10 subpod was linked with AI pod (PCC=4) before being linked with other members of AB pod. AI pod frequently traveled with AB pod early in the study, and we suspect that AI pod (7 whales in 1996) was in the final stages of a gradual split from the then 35-member AB pod when the study began in 1984. AI pod traveled more independently of AB pod in later years. The pod-specific dialects for AI and AB pods are very similar (Ford[1]), supporting this hypothesis. The preponderance of adult males in AI pod (4 out of 7 whales in 1996) may have contributed to the independence of this matrilineal group. Bigg et al. (1990) found that matrilineal groups with a high percentage of males tend to travel more independently. This was also evident for the AB10 subpod, in which 3 out of 4 members were adult males. AB10 subpod often traveled a distance away from the remainder of AB pod.

Direct observation and photographic analysis also indicated that some males

[1] Ford, J. K. B. 1997. Vancouver Public Aquarium, P.O. Box 3232, Vancouver, B.B., Canada. Personal commun.

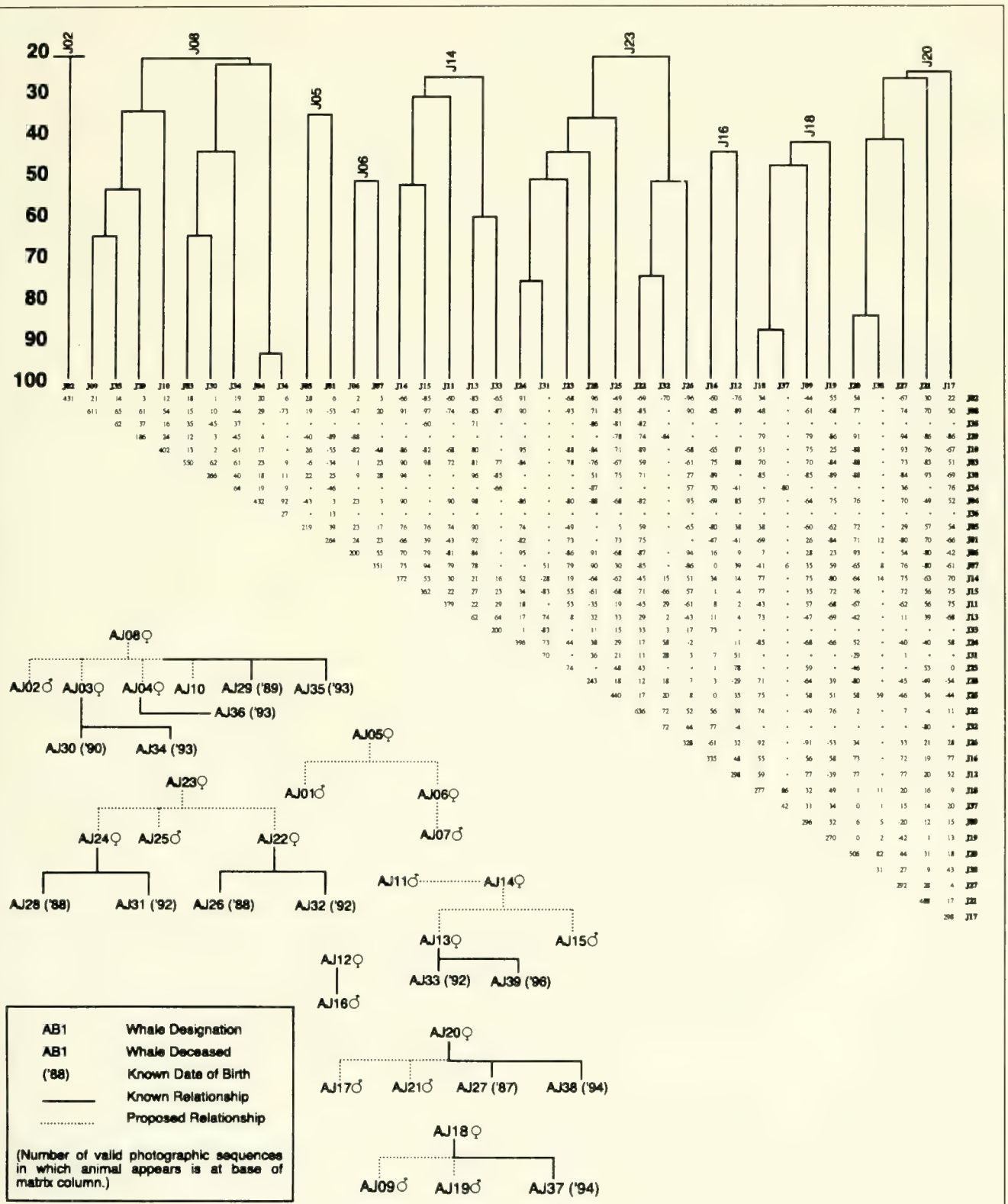

Figure 9

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AJ pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

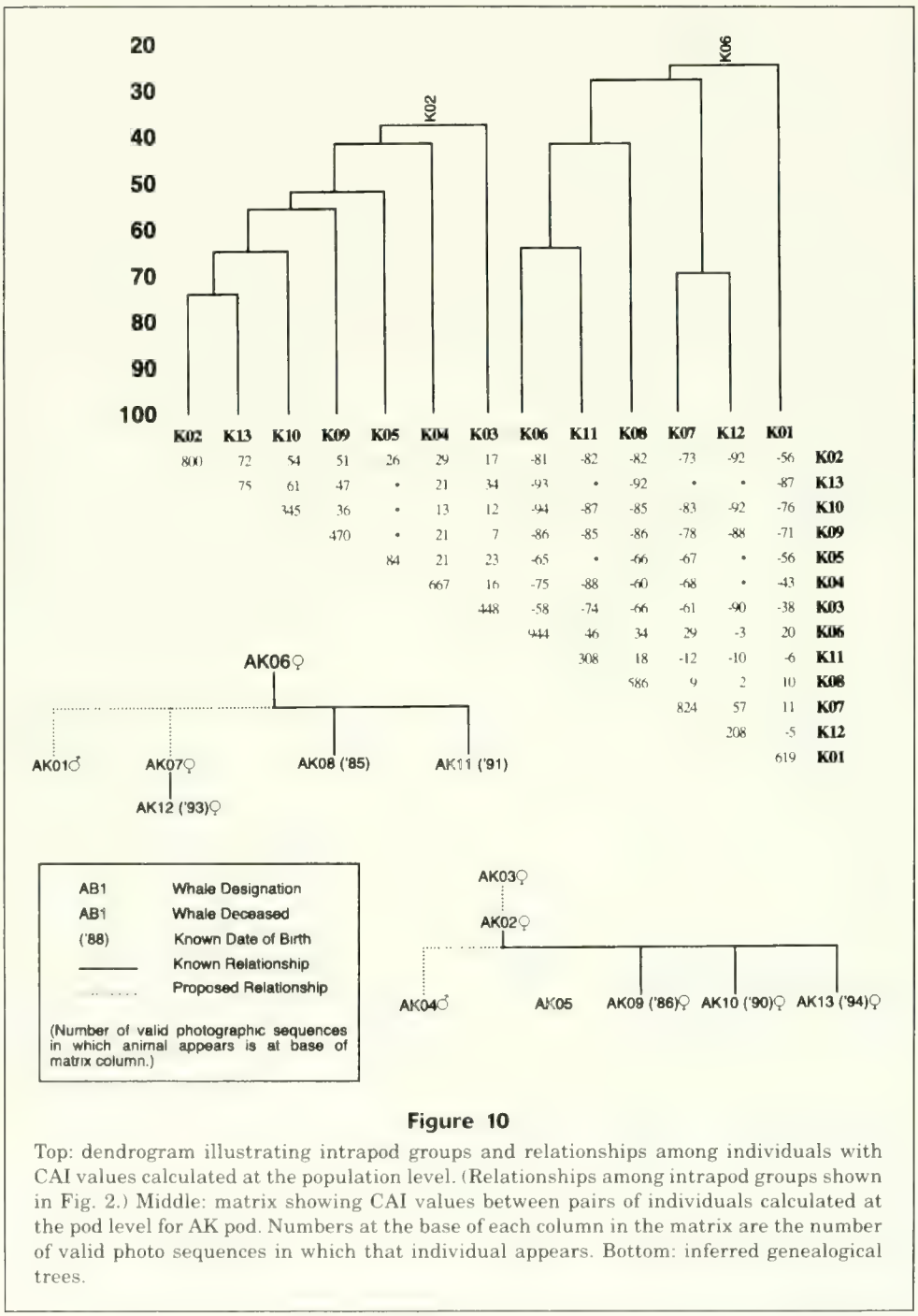

Figure 10

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AK pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

occasionally traveled with other adult or juvenile males or traveled independently, particularly during the multipod encounters observed in July and August (Matkin et al., 1997). In two cases, pairs of males were more highly associated with each other than with any other intrapod groups.

We witnessed the splitting of one pod (AN pod into AN10 and AN20 pods) during the course of the study. This was not a gradual occurrence, as suggested by Bigg et al. (1990) for A04, C01, and D01 pods in British Columbia but appeared to be a rather abrupt event around 1989. The pod split along intrapod (matrilineal) groups, while all 13 of the intrapod groups in the two pods remained intact. AN pod numbered 35 whales at the time it split and was the largest pod in the study at that time.

Bigg et al. (1990) defined subpods as fragments of pods that occasionally split and traveled separately

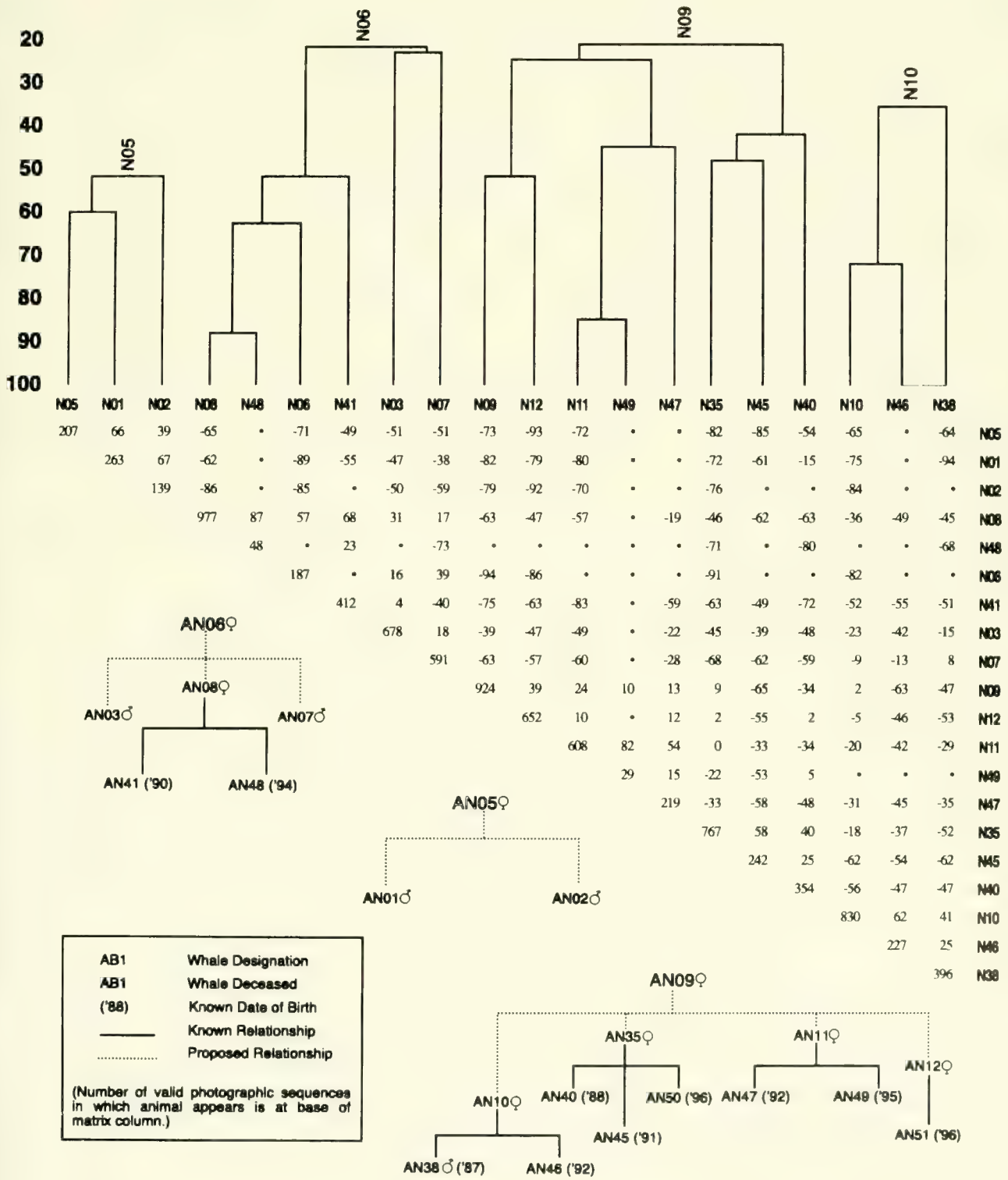

Figure 11

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN10 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

from their pods. Through association analysis, we expanded this definition to include groups that travel in unison with their pod but rarely mix with other groups within the pod. This latter situation occurred only for AB pod, which was divided into three subpods. By direct observation and examination of

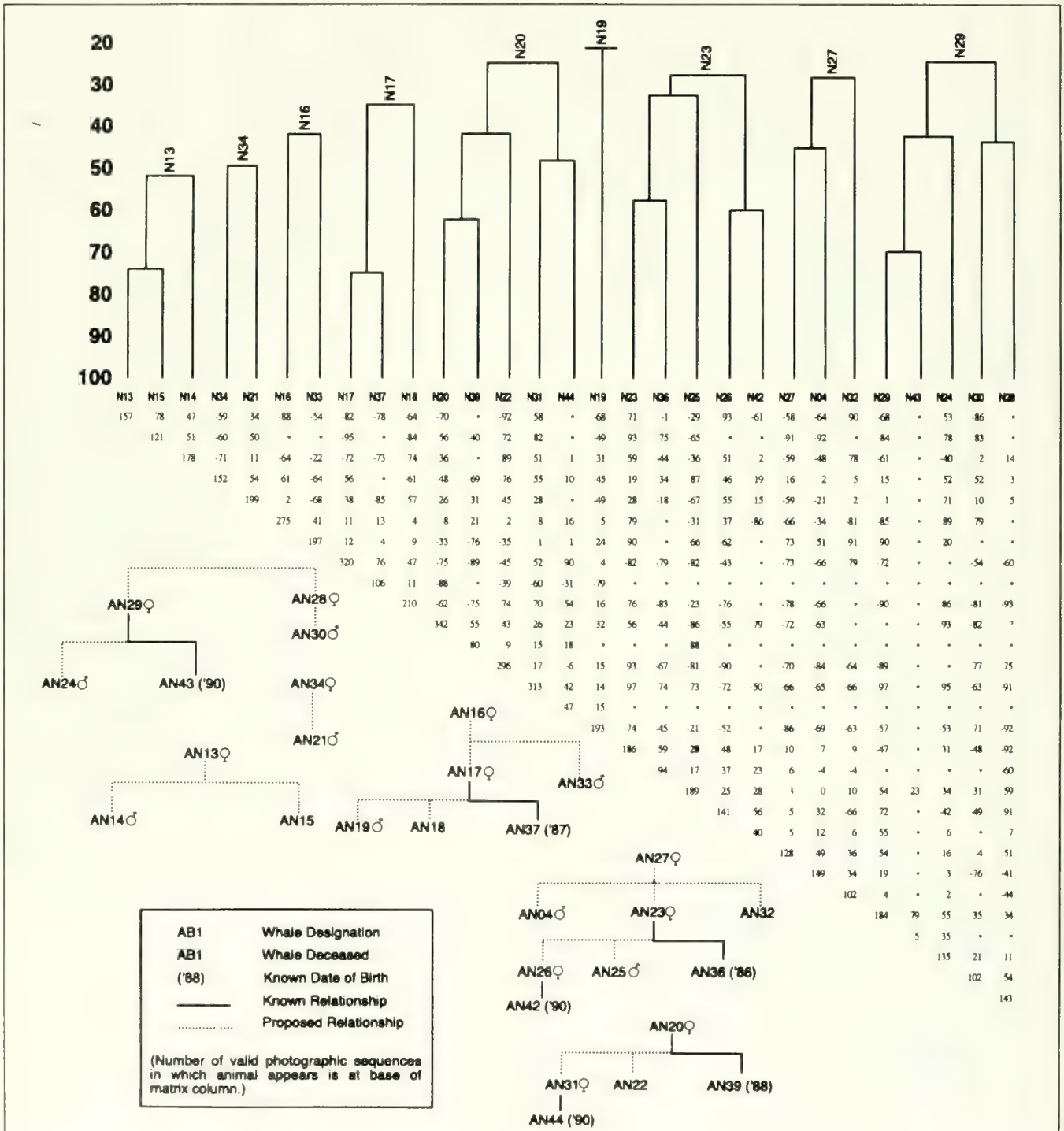

Figure 12

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN20 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

photographs of this pod, it was determined that AB pod nearly always traveled as a unit; however, in the dendrogram linking intrapod groups (Fig. 2) it appeared as three separate groups (PCC>0). This finding indicated that although they were traveling together, the subpods tended not to mix with the rest of the pod.

Communities were described by Bigg et al. (1990) as closed populations of pods that associated with one another. They described two geographically distinct communities of resident killer whales (northern and southern residents) that had separation in range near the middle of Vancouver Island, British Columbia. We found no separation of pods into communities by this definition in our area, although our study discerned matrilineal (intrapod) groups, subpods, and pods. Resident whales from AF and AG pods photographed regularly in southeastern Alaska were observed swimming with the pods described in this study (Matkin et al., 1997). One of the pods described in this paper, AD5 pod, was photographed off Kodiak Island. It thus appears that geographic boundaries do not delineate communities for resident killer whales from southeastern Alaska to Kodiak Island.

The association analysis for individuals within pods strongly suggested that strength of bond was directly correlated to degree of relatedness. There was only one case in which statistical analysis indicated that offspring born during the study did not maintain the strongest bond with its mother. The mother AB8 and her sibling AB18 both died at the time of the Exxon Valdez oil spill. AB8 left her year-old offspring, AB41 (born 1988). Association analysis indicated that AB41 was more closely linked (CAI=58) to its mother's apparent sibling, AB18, than to its mother, AB8 (CAI=50); the young whale AB41 died several years later (1993–4).

Five whales that were juveniles at the beginning of the study were most closely associated with whales other than their mothers. Three were females, AK07, AN08, and AN11, each of which produced offspring during the study. Following these births, they were more closely bonded to their offspring rather than to their own mothers. This finding demonstrates that new mothers, when they produce calves, develop distance from their own mothers (Table 4). The tendency of females with offspring to travel farther from their mothers than the distance prior to first reproduction suggests a process of separation that may also be basic to new pod formation.

Our proposed genealogical trees suggest that intrapod groups are matrilineal groupings of mothers and their descendants (Figs. 1 and 3–12). There was no immigration or emigration of male or female offspring from these natal groups over the course of our study. These extremely stable matrilineal groups appear to be the foundation of resident pod social structure in Prince William Sound. This is similar to results from studies in British Columbia and Washington State (Bigg et al., 1990).

We were most confident in genealogical trees for pods that were most frequently photographed, such as AE and AK pods, and less confident in trees for the much less frequently observed AD5 and AD16 pods. The large number of mortalities in AB pod also made construction of genealogical trees more difficult. The greatest potential source of error in genealogical assignment was the death of the mother of a young whale prior to the study, in which case the young whale would likely travel with its closest female relative. However, since the annual natural mortality rate for reproductive females is extremely low (0.0048 according to Olesiuk et al., 1990), this source of error was probably insignificant except following disasters such as the high loss of reproductive females after the Exxon Valdez Oil Spill (Matkin et al., 1994).

In all but one of the resident pods we examined, the total number of whales increased over the period of the study, indicating that a majority of matrilineal groups have been growing or dividing (or doing both) over the past decades. The exception was AB pod, which declined during this period from 35 to 23 whales (28 deaths; 16 births). Six of the mortalities occurred during 1985 and 1986 when there was a conflict with the sablefish (*Anaplopoma fimbria*) fishery (Matkin et al., 1994). During this period apparent bullet wounds were observed in 16 whales.

Fourteen of the mortalities in AB pod occurred in the year and a half following the 1989 Exxon Valdez oil spill (Matkin et al., 1994). Some of the matrilineal groups in the pod are nearly extinct as a result of these deaths. An adult male, AB03, appears to be the last member of a once-large matrilineal group linked by the apparent sisters AB06 and AB07 (Fig. 1; AB03 has since died). Another large matrilineal group (matriarch AB09) has been reduced to a single orphaned 5-year-old, AB45. Many of the mortalities have been those of juveniles (13) or reproductive females (4) and have severely reduced the reproductive potential of the pod.

The statistical support for the existence of intrapod groups and the apparent lack of emigration or immigration into these groups allows for determination of demographic changes, both natural and induced, within resident killer whale populations. The detailed delineation of social structure in resident killer whales provides a unique opportunity for monitor-

ing and modeling of these populations. This situation appears to be unique among social mammals (e.g. the lack of male dispersal), with the possible exception of the long-finned pilot whale. In that species, molecular typing revealed that pod members also form extended family groupings from which individuals do not disperse (Amos et al., 1993). Molecular typing of individual whales described in this study is currently in progress (Barrett-Lennard[2]).

Acknowledgments

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Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the Southern California Bight

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Abstract.—We studied fine-scale vertical distribution of northern anchovy, *Engraulis mordax*, eggs and larvae and larvae of associated species at two stations off southern California in March–April 1980 using a Manta (neuston) net and a MESSHAI (multiple opening-closing net) sampler. A pump and fluorometry system was used to obtain chlorophyll profiles. A storm with associated heavy seas interrupted sampling for two days at the inshore station and provided an opportunity to compare pre- and poststorm egg and larval distribution and abundance. A total of 95,552 fish larvae were taken in the MESSHAI (63 tows) and Manta nets (41 tows), representing 49 taxa (genera or species) in 27 families. *Engraulis mordax* was the most abundant fish (95% of the total), followed by *Leuroglossus stilbius*, *Genyonemus lineatus*, *Stenobrachius leucopsarus*, *Sebastes* spp., *Seriphus politus*, *Peprilus simillimus*, *Paralichthys californicus*, *Citharichthys* spp., and *Merluccius productus*. Anchovy eggs and larvae had a shallow distribution: 90% of larvae and 95% of eggs were found in the upper 30 m. Peak egg density was found in the neuston; peak larval density, in the 10–20 m stratum. Larvae of shallow-living shelf species (*G. lineatus*, *P. simillimus*, *P. californicus*) typically occurred in the upper 20–30 m, whereas larvae of predominantly deeper-living demersal species (*Sebastes* spp., *M. productus*) were found in the upper 80 m. Midwater species (*L. stilbius*, *S. leucopsarus*) occurred at least to 200 m. Anchovy eggs decreased in number after the storm. Anchovy larvae declined even more sharply, despite an increase in zooplankton and potential larval fish prey, suggesting that starvation may have resulted from disturbance of microscale food patches. Alternatively, larvae may have been advected away from the site. Shallow-water shelf species were rare at the inshore station before the storm but appeared suddenly afterwards as a result of seaward advection of shelf water by Ekman transport.

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The use of ichthyoplankton techniques for estimating the biomass of fish stocks has increased markedly over the past two decades (Hunter and Lo, 1993). Information on the horizontal and vertical distribution of eggs or larvae of a target species is a requirement for quantitative sampling of these stages and for interpreting data from integrated net tows and from recently developed samplers such as the continuous underway egg pump (Checkley et al., 1997). The daily egg production method (DEPM) was developed at the Southwest Fisheries Science Center to provide annual biomass estimates needed to manage northern anchovy, *Engraulis mordax*, an important coastal pelagic species inhabiting the California Current region (Lasker, 1985). During the development of this method a cruise was conducted off southern California that employed a MESSHAI, a sampler with opening-closing nets and environmental sensors, to determine fine-scale vertical distribution of eggs and larvae of *E. mordax* (see preliminary data in Pommeranz and Moser, 1987). This information was needed to supplement Ahlstrom's (1959) vertical distribution study based on 22 Leavett net tows taken on 9 cruises over a 14-year period off southern California and Baja California. The MESSHAI study supplied information on depth, ambient temperature, and diurnal periodicity of *E. mordax* eggs needed to develop the DEPM (Lasker, 1985). To compare distributions at different bottom depths, sampling was conducted at two localities: an offshore site over the Santa Catalina Basin and an inshore site over the upper continental slope off Dana Point, California. Anchovy larvae, the dominant species in the MESSHAI samples, were counted and measured for subsequent growth and mortality studies. A storm interrupted sampling at the inshore station and provided an opportunity to study the influence of water column disturbance on the abundance and depth distribution of eggs and larvae of anchovy and associated species. Mullin et al. (1985) described the effects of this storm on the abundance and vertical structure of phytoplankton, zooplankton, and total fish larvae on the basis of pump samples taken at the same time as the MESSAI sampling at a locality

just shoreward of the inshore MESSHAI site.

This paper presents a preliminary analysis of the fine-scale vertical distribution of anchovy eggs and larvae and the larvae of other taxa, with comparisons of the offshore and inshore sites and of the prestorm and poststorm periods at the inshore site. A separate paper addressing age-specific vertical distribution and mortality of anchovy eggs and larvae is in preparation.

Methods and materials

Cruise 8003-EB was conducted aboard RV *Ellen B. Scripps* at two sampling sites in the Southern California Bight (SCB; Fig. 1). The first site (33°11.1'N, 118°16.5'W), occupied 19–27 March 1980, was located 13 km south of the east end of Santa Catalina Island, over an ~1150 m bottom depth. This site lies over the Santa Catalina Basin, one of 13 deep basins that characterize the offshore region of southern California (Ebeling et al., 1970; Eppley, 1986). The midwater fish fauna of these basins is a mix of subarctic, transitional species of the California Current and species from the eastern tropical Pacific and central water masses whose distributions extend into the region. The site is close enough to Santa Catalina Island to have larvae of shelf species (Hobson and Chess, 1976) in addition to larvae of slope and basin floor species (Cross, 1987). The second site (33°28.5'N, 117°47.0'W), occupied 29 March–6 April 1980, was ~4.5 km off Dana Point, over the upper continental slope at approximately 430 m bottom depth. Here the adjacent shelf narrows to a minimum of about 3 km but supports rich fish communities associated with rocky reefs and kelp forests (Feder et al., 1974; Cross and Allen, 1993) and soft-bottom habitats (Mearns, 1979; Love et al., 1986; Allen and Herbinson, 1991; Cross and Allen, 1993). The continental slope, also relatively narrow here, supports a fish assemblage typical of other southern California slope regions (Cross, 1987). The first site corresponds to California Cooperative Oceanic Fisheries Investigations (CalCOFI) station 90.2, 35.8 and the second to station 90.0, 28.2. Sampling at the offshore station was interrupted twice by heavy seas (0055, 21 March to 0908, 23 March; and 1730, 26 March to 0836, 27 March). A storm with associated heavy seas curtailed sampling at the inshore site at 0315, 1 April; the station was reoccupied at 0655, 3 April.

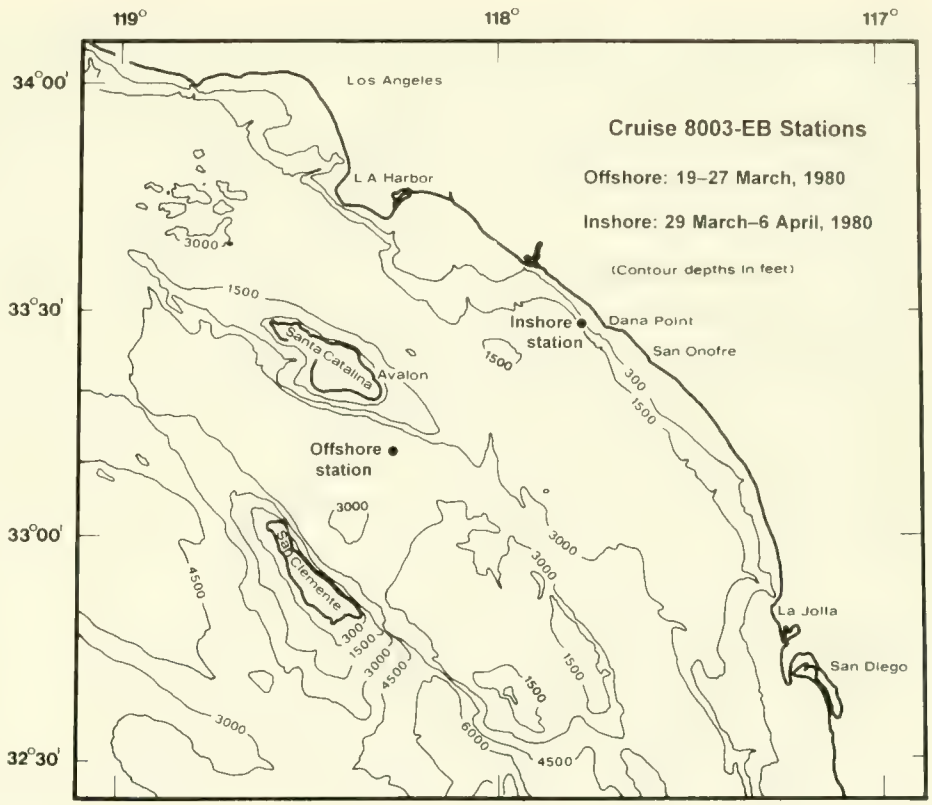

Figure 1

The Southern California Bight, showing stations occupied on Cruise 8003-EB (modified from Shepard and Emery, 1941).

The principal samplers used were the Manta net (Brown and Cheng, 1981) for sampling the surface layer (0–15.5 cm) and the MESSHAI for sampling discrete depth strata in the upper 200 m. The MESSHAI sampler was a modified Gulf-V sampler (Arnold, 1959; Nellen and Hempel, 1969) with a 25×25 cm mouth opening, six opening and closing nets operated from a computer deck unit, and an environmental sensing package (Pommeranz and Moser, 1987). All nets were fitted with 300-μm mesh. A sampling sequence for a day or night station consisted of a five-minute Manta tow, followed by an oblique MESSHAI tow that sampled 10-m strata from 50 m to the surface, an oblique MESSHAI tow which sampled 40-m strata from 200 m to the surface, a second MESSHAI tow which sampled 10-m strata from 50 m to the surface, and a second Manta tow. A total of 17 Manta tows (10 day, 7 night) were taken at the offshore station, 24 (13 day, 11 night) at

the inshore station (Figs. 2 and 3). All MESSHAI tows were stepped oblique hauls. In the shallow tows the sampler was lowered to 50 m and retrieved through five 10-m strata, each in 2.5-m steps lasting two minutes, with a total of five horizontal phases per stratum. Depth, temperature, and flowmeter profiles were recorded by the deck unit throughout each tow. Bucket surface temperatures were taken periodically to calibrate the MESSHAI temperature sensor. In the deep tows the sampler was lowered to 200 m and retrieved through five 40-m strata, each in five steps lasting two minutes. The total number of successful MESSHAI tows was 24 (shallow: 9 day and 8 night; deep: 4 day and 3 night) at the offshore station and 36 (shallow: 12 day and 12 night; deep: 6 day and 6 night) at the inshore station. Improper preservation or breakage resulted in the loss of anchovy eggs in net 4 (20–30 m stratum) of tow 42 and the entire sample from net 3 (30–40 m stratum) of tow 61. Three MESSHAI tows were unsuccessful owing to technical difficulties, and the samples were subsequently discarded. All tows were made at a ship speed of ~1.5 knots. Before each net tow series at the inshore station, a pump and fluorometry system (Lasker, 1978) was used to obtain a chlorophyll profile down to 40 m depth. Water samples were taken at the surface and at the chlorophyll maximum for chlorophyll-*a* and phaeophytin extraction and fluorometry, and for identification and counts of major phytoplankton taxa (analyses not included in this paper). Oblique bongo net samples were taken at each station at a ship speed of about 1.5 knots; except for length-frequency information, data from these tows are not addressed in this paper.

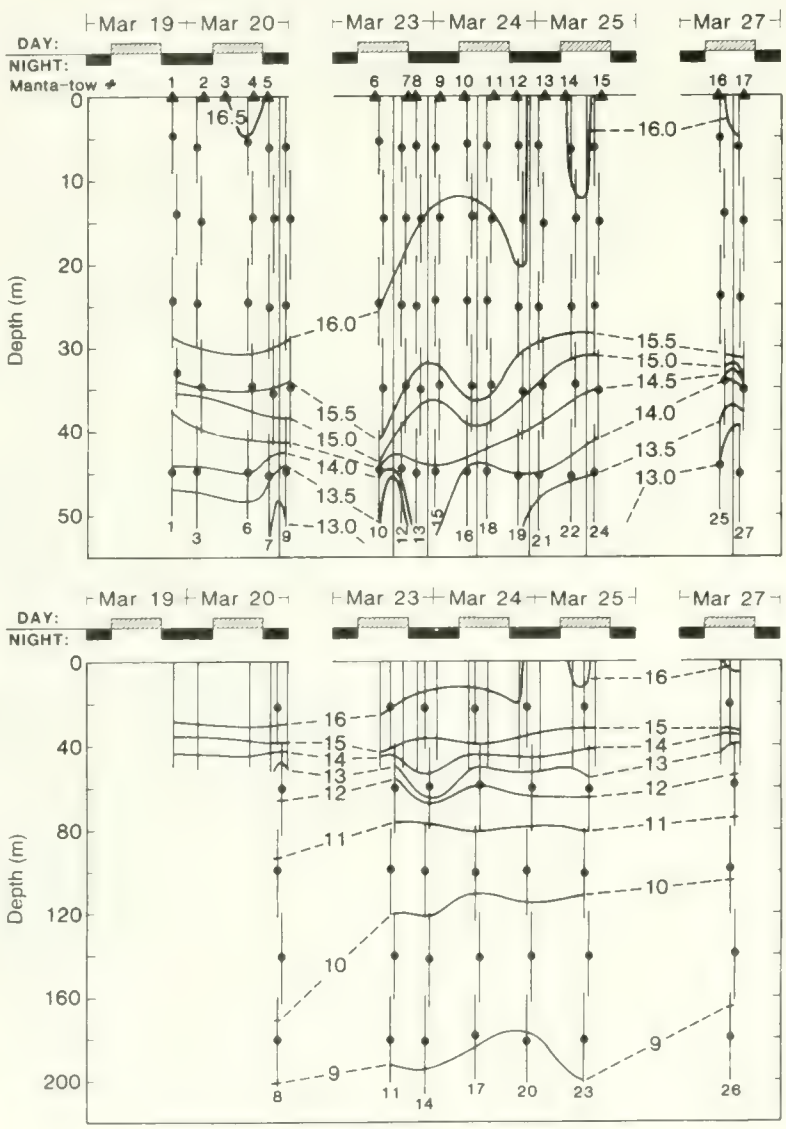

Figure 2

Diagram showing chronology of MESSHAI tows, depth strata sampled, and isotherms for the offshore station (from Pommeranz and Moser, 1987). (**Above**) Shallow (50 m) and Manta tows; the dots represent average depths for each net; the seven complete vertical lines show when deep (200 m) tows were taken. Tow numbers for Manta tows are given above solid triangles and tow numbers for MESSHAI tows are given at the bottom of each series of vertical lines. Isotherms are shown in 0.5 C intervals. (**Below**) Deep tows; the 17 lines extending down to 50 m indicate when shallow tows were taken. Isotherms are shown in 1 C intervals.

Most samples were preserved in 5% buffered formalin; selected samples were preserved in 80% ethyl alcohol for analysis of otolith daily growth rings in anchovy larvae. Prior to sorting, wet zooplankton displacement volume of each sample was measured using standard techniques (Kramer et al., 1972). Anchovy larvae and eggs were identified and removed during the plankton sorting process; eggs were classified by stage according to the criteria of Moser and Ahlstrom (1985) and length measurements of larvae were taken to the nearest 0.5 mm. Larvae of other fish were identified to the lowest taxon possible

and body lengths were measured to 0.1 mm.

We used analysis of variance (ANOVA) to compare the pre- and poststorm densities of anchovy eggs and larvae for shallow strata and also for deep strata at the inshore and offshore stations. Day and night data were pooled for each of these categories because the data did not indicate a diurnal shift in vertical distribution of eggs or larvae. All data were log-transformed for statistical analyses because the original data were highly skewed. Data from the shallow strata included the Manta tows, the MESSHAI shallow tows (0–50 m), and the upper 40 m from the MESSHAI deep tows. Data for the deep strata were from below 40 m from the deep MESSHAI tows. A two-way ANOVA was performed for the shallow strata, the two factors being station (inshore and offshore) and tow type (Manta, MESSHAI shallow, and MESSHAI deep). Interaction terms were included in the analysis. One-way ANOVA was performed for data from the deep strata to compare anchovy larval density at inshore and offshore stations.

In the analysis of prestorm and poststorm conditions two separate ANOVAs were performed because an initial ANOVA of anchovy eggs from the shallow strata indicated a strong interaction between tow type and pre- or poststorm period; one analysis was based on data from shallow and deep MESSHAI tows and the other was based on Manta tows only. A single two-way ANOVA test was performed for anchovy larvae because the density of anchovy larvae in Manta tows was low and the analysis adequately described the effect of the storm on larval density based on both shallow and deep MESSHAI tows.

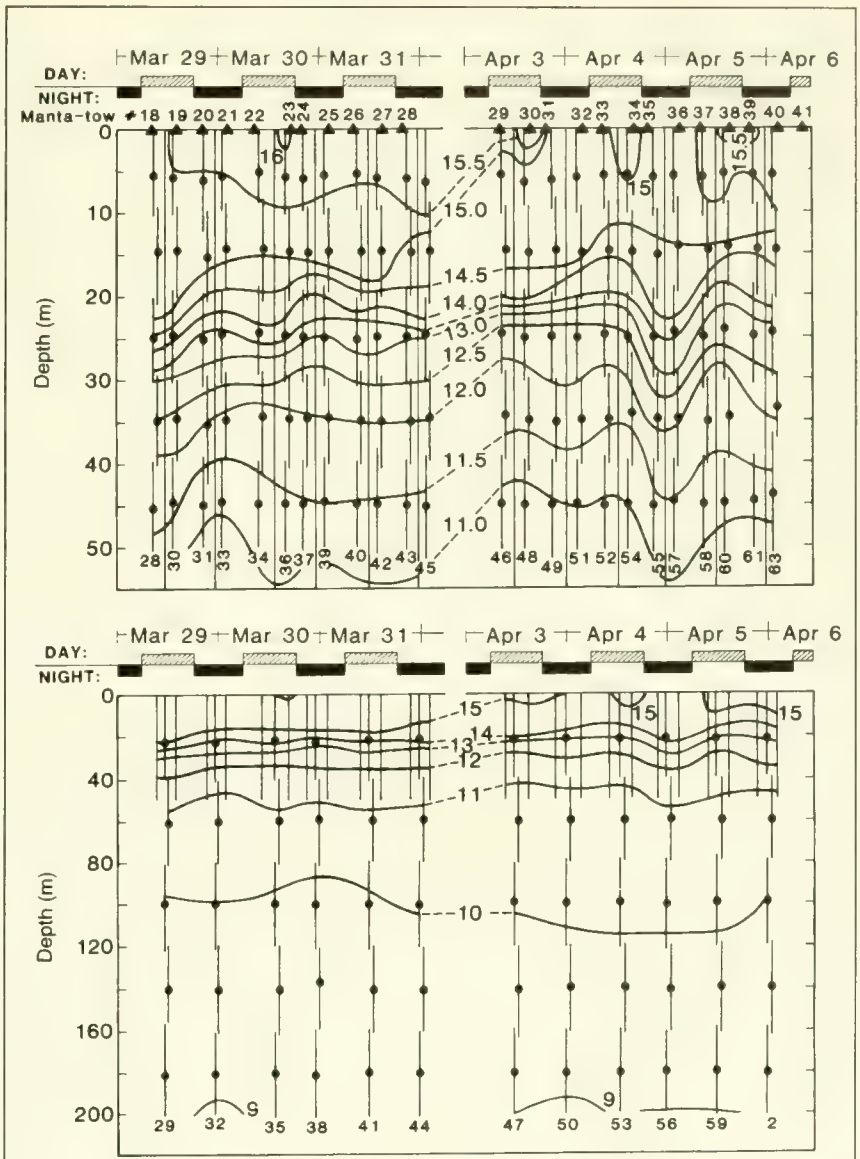

Figure 3

Diagram showing the chronology of MESSHAI tows, depth strata sampled, and isotherms at the inshore station. Symbols and labels are the same as those in Figure 2 (from Pommeranz and Moser, 1987).

Results

Environmental features

The thermal structure of the study area was typical for March–April in that region of the SCB, with a pool of relatively warm water subject to intrusions of advected upwelling plumes from the Point Conception area (Lasker et al., 1981; Lynn et al., 1982). The mixed layer was about 30–40 m deep at the offshore station (Fig. 2) and only about 10–30 m deep at the inshore station (Fig. 3). Overall, the water was colder at the inshore station, which lacked the prominent 16.0° isotherm present offshore. Average temperature was higher at the offshore station in all depth strata except 160–200 m (Fig. 4, A and B). At the inshore station after the storm the thermocline shoaled to 15–20 m and water temperature was lower

than before the storm at all depths below 80 m (Figs. 2; 3; 4, C and D).

Wind and sea-state observations taken during the cruise and supplemented by data from the Naval Air Station at San Clemente Island, southwest of the offshore station, and the San Onofre Nuclear Generating Station, just southeast of the inshore study area (Fig. 1), indicated an oscillating land-sea system which was more evident at San Onofre than at San Clemente (Fig. 5). During the night and morning, winds typically were from the NNE, after which they shifted through the south to the NW until late afternoon or evening. Average wind speed was about 10 knots at the offshore station and about 6 knots at the inshore station; average swell height was about 1.7 m and about 1 m at the two sites, respectively (Fig. 6). At the inshore station wind speed was more than 24 knots during the storm.

Prior to the storm at the inshore station there was a moderate to strong chlorophyll maximum at 18–29 m (Fig. 7). Following the storm, the chlorophyll peak became shallower and generally broader. The peak was at 15 m on the morning of 3 April; by the evening of 4 April, the maximum was near the surface. On the following two days the peak reappeared and began to deepen and strengthen. Average plankton volumes of Manta and MESSHAI samples from the upper 40 m were distinctly higher at the inshore station than at the offshore station (Fig. 8, A and B). Average volumes were generally higher in strata within the upper 40 m in poststorm samples compared with those taken prior to the storm (Fig. 8, C and E). Average plankton volume increased markedly in the 40–80 m stratum, whereas there was little change in deeper strata (Fig. 8E).

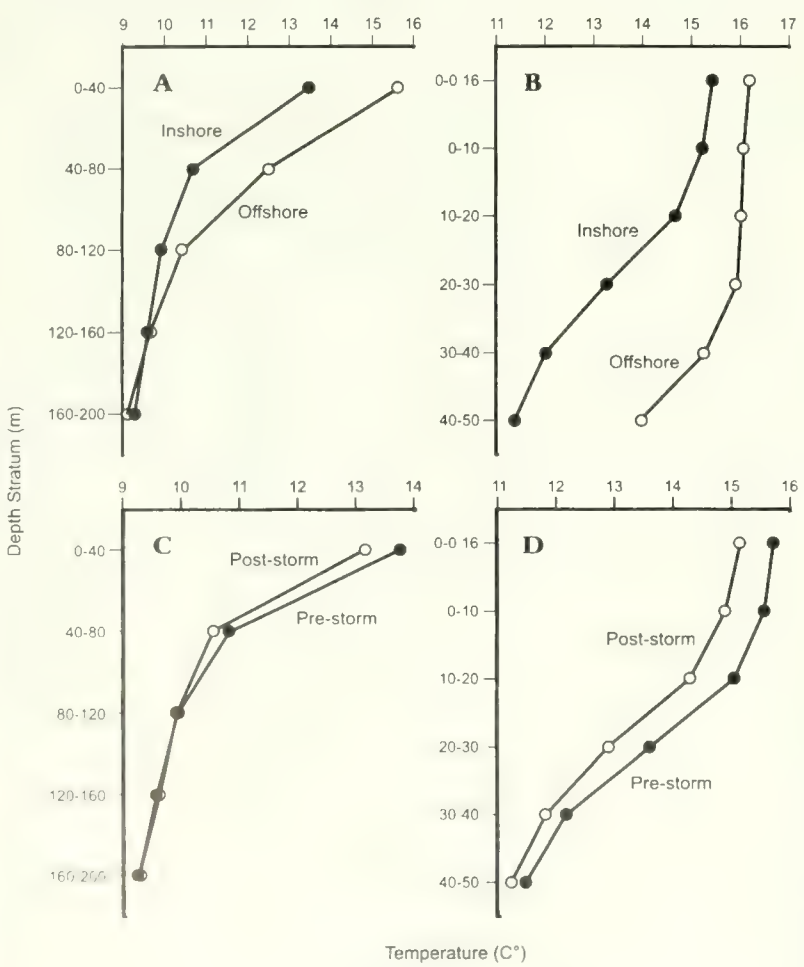

Figure 4

Average temperatures for strata sampled with the MESSHAI, based on data from the MESSHAI temperature sensor. (**A**) Deep tows at inshore (dots) and offshore (circles) stations; (**B**) shallow tows at inshore (dots) and offshore (circles) stations; (**C**) deep tows at inshore station before the storm (dots) and after the storm (circles); (**D**) shallow tows at inshore station before the storm (dots) and after the storm (circles).

Engraulis mordax eggs

A total of 67,157 *E. mordax* eggs were collected in the MESSHAI and Manta nets. Anchovy eggs had a slightly shallower distribution than larvae, with approximately 95% of eggs in the upper 30 m (Fig. 9, A and B). In shallow strata (including Manta, shallow MESSHAI, and the 0–40 m stratum of the deep MESSHAI tows), average density was greater at the offshore station than at the inshore station ($F_{1,95}$=4.72, P=0.003). Yet egg density in the deep strata was similar at the two stations. Average egg density in the surface layer was more than double that in the 0–10 m stratum (Fig. 9B). In the shallow strata at the inshore station, egg densities in MESSHAI tows were reduced after the storm ($F_{1,32}$=12.73, P=0.001), whereas egg densities did not change much in Manta tows ($F_{1,22}$=1.58, P=0.048) and in deep (>40 m) MESSHAI tows ($F_{1,10}$=2.67, P= 0.132) (Fig. 9, C and F).

Fish larvae

A total of 95,552 fish larvae were taken in the MESSHAI and Manta nets,

Figure 5

Wind direction and speed during Cruise 8003-EB based on data from San Onofre Nuclear Generating Station, the Naval Air Station on San Clemente Island, and observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1987).

representing 49 taxa (genera or species) in 27 families; 90,402 (95% of the total) were northern anchovy, *Engraulis mordax* (Table 1). Anchovy larvae were more than 40 times as abundant as the next most abundant species, California smoothtongue (*Leuroglossus stilbius*). White croaker (*Genyonemus lineatus*) ranked third, and the northern lampfish (*Stenobrachius leucopsarus*) ranked fourth, followed by the rockfish genus *Sebastes*. These five taxa constituted 99% of the total larvae. Following in abundance were queenfish (*Seriphus politus*), Pacific pompano (*Peprilus simillimus*), California halibut (*Paralichthys californicus*), the sanddab genus *Citharichthys*, and Pacific hake (*Merluccius productus*) (Table 1).

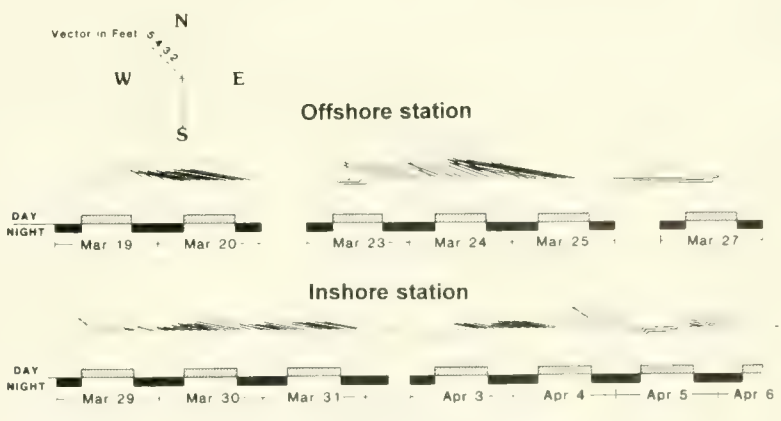

Figure 6

Swell direction and height during Cruise 8003-EB from observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1986).

Most of the larvae captured in the MESSHAI nets were at yolksac and preflexion stages. Relatively fewer anchovy larvae <3.0 mm and relatively more anchovy larvae >3.0 mm were taken by the bongo

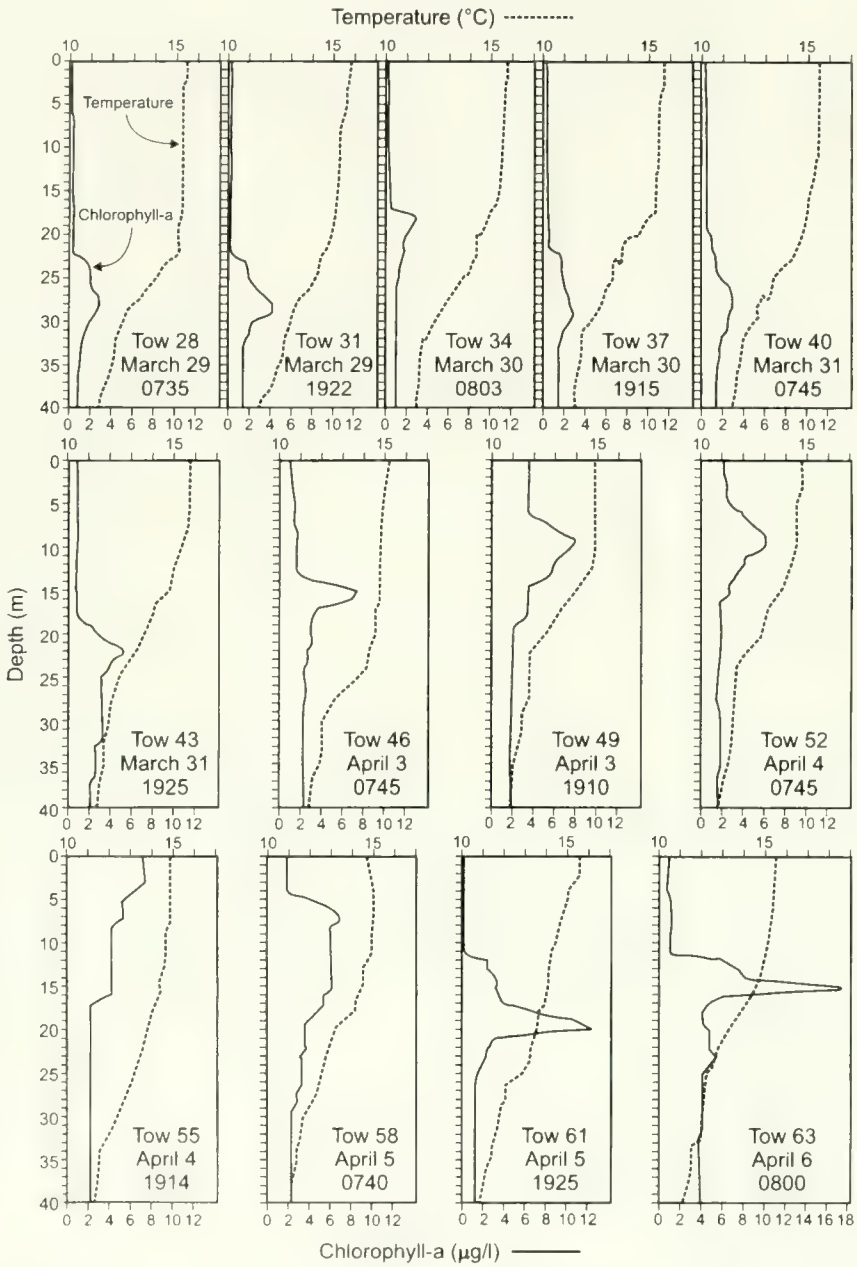

Figure 7

Chlorophyll-*a* (µg/l) and temperature (°C) profiles at the inshore station on Cruise 8003-EB. Tow numbers are given for shallow MESSHAI tows from which temperature profiles were derived.

net than in the MESSHAI tows (Fig. 10, A and B). The length-frequency distribution of larvae captured by the Manta net was bimodal, with peaks at 3.0 and 7.0 mm (Fig. 10C). For species other than northern anchovy, length distributions generally were similar for larvae caught in Manta and MESSHAI nets. Exceptions were a sample of 38 *Sebastes* spp. larvae captured in Manta net tow 18 (length range 5.0–9.4 mm, average length 7.2 mm) and an 8.0 mm presettlement *Paralichthys californicus* larva captured in Manta tow 31.

***Engraulis mordax* larvae** Anchovy larvae had a shallow distribution, with approximately 90% of the larvae in the upper 30 m (Fig. 11, A and B). In shallow strata, average larval density was greater at the

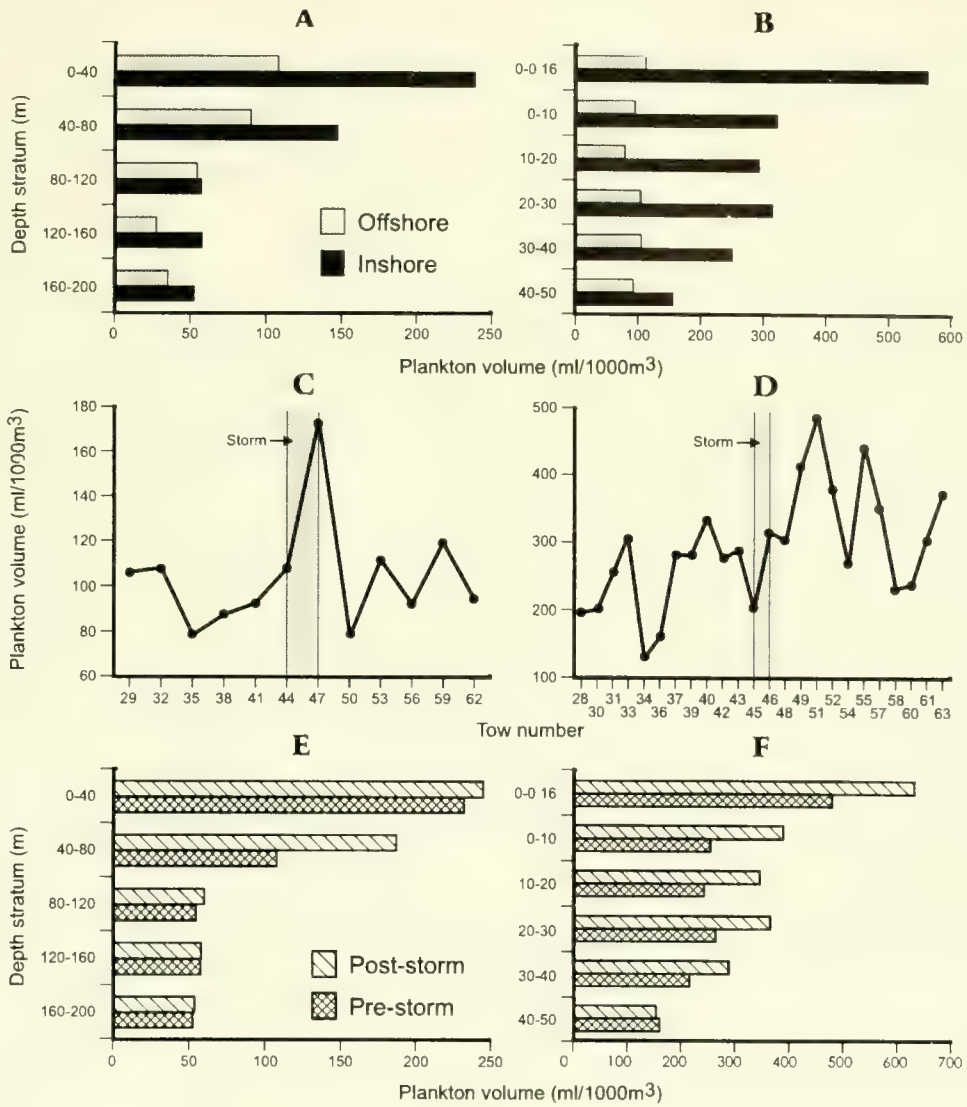

Figure 8

Plankton volumes (mL/1000 m³) in MESSHAI tows. Average volumes from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) volumes in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) volumes in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

inshore station than at the offshore station (Fig. 11A; ANOVA of shallow strata, $F_{1,95}$=31.78, P=0.003). Within the upper 50 m at the inshore station, average density was highest in the 10–20 m stratum, accounting for approximately 40% of larvae. Density in the surface layer was comparatively low. In deep strata no significant difference in larval density was found between inshore and offshore stations ($F_{1,17}$=0.53, P=0.47). At the inshore station, average larval densities were lower in poststorm samples than in prestorm samples (shallow strata: $F_{1,54}$= 11.21, P=0.001; deep strata: $F_{1,10}$=10.05, P=0.001). Overall, larval distribution was somewhat shallower after the storm (Fig. 11, E and F).

***Leuroglossus stilbius* larvae** In deep MESSHAI tows, larvae of *L. stilbius* occurred in relatively high densities in most strata down to 200 m (Fig. 12A). The lower limit of their distribution was not determined by the MESSHAI samples, but another study

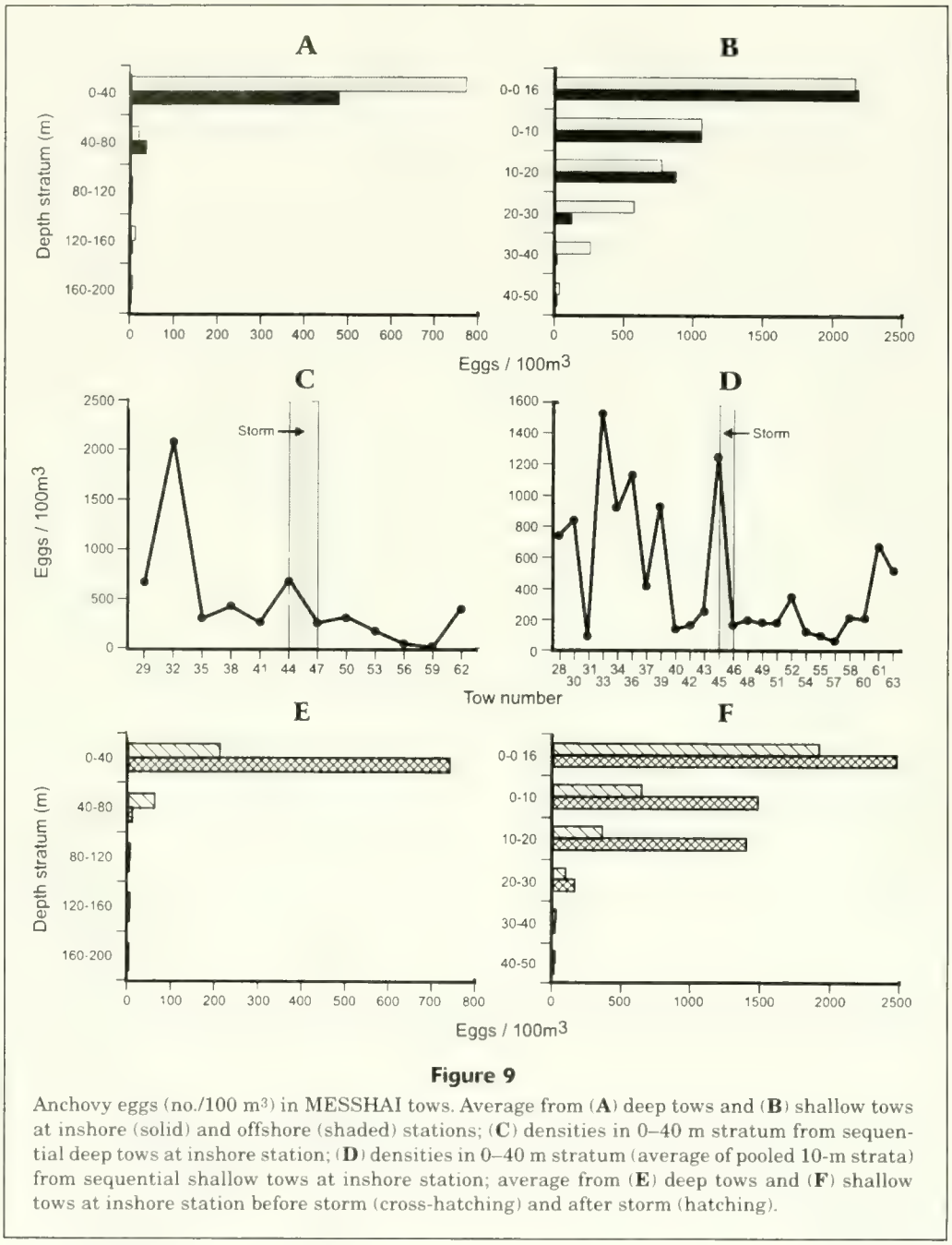

Figure 9

Anchovy eggs (no./100 m³) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

(Moser and Smith, 1993) showed that they may occur down to 300 m. Average densities were generally higher at the inshore station than at the offshore station. Larvae were absent from the 0–40 m stratum offshore and were nearly absent from this stratum in prestorm inshore samples (Fig. 12, A and E). In samples at the inshore station, average densities following the storm increased markedly at 0–80 m, decreased at 80–160 m, and increased slightly in the 160–200 m stratum (Fig. 12E). Larvae were not taken in Manta tows nor in the upper 40 m of shallow MESSHAI tows at the offshore station (Fig. 12B). At the inshore station the distribution was shifted upward in poststorm samples and average larval densities were relatively high in strata as shallow as 30–40 m (Fig. 12F).

***Genyonemus lineatus* larvae** White croaker larvae were absent from offshore samples and were abundant only in the upper 30 m at the inshore station (Fig. 13, A and B). Average densities were extremely low in prestorm samples but were relatively high in

Table 1

Taxa captured by Manta and MESSHAI nets on Cruise 8003-EB. Numbers of larvae are unadjusted counts; occurrences are listed in parentheses with onshore occurrences to the left of the slash and offshore occurrences to the right. Only taxa identified to genus or species are included.

Taxon	Family	Number of larvae and occurrences			
		Manta	Shallow MESSHAI	Deep MESSHAI	Total
Engraulis mordax	Engraulidae	3,066 (24/15)	67,640 (24/17)	19,696 (12/7)	90,402 (99)
Leuroglossus stilbius	Bathylagidae	0	785 (22/2)	1,401 (12/7)	2,186 (43)
Genyonemus lineatus	Sciaenidae	49 (7/0)	740 (19/0)	173 (8/0)	962 (34)
Stenobrachius leucopsarus	Myctophidae	1 (0/1)	349 (24/9)	193 (12/7)	542 (53)
Sebastes spp.	Sebastidae	53 (3/0)	264 (22/12)	134 (10/7)	441 (54)
Seriphus politus	Sciaenidae	17 (6/0)	164 (12/0)	106 (5/0)	287 (23)
Peprilus simillimus	Stromateidae	6 (4/0)	180 (21/2)	35 (10/0)	221 (37)
Paralichthys californicus	Paralichthyidae	9 (3/0)	82 (16/0)	23 (6/0)	114 (25)
Citharichthys spp.	Paralichthyidae	0	63 (17/1)	14 (7/1)	77 (26)
Merluccius productus	Merlucciidae	0	36 (15/0)	12 (5/4)	48 (24)
Atherinopsis californiensis	Atherinidae	44 (9/0)	0	0	44 (9)
Pleuronichthys verticalis	Pleuronectidae	1 (1/0)	25 (9/0)	8 (3/0)	34 (13)
Lyopsetta exilis	Pleuronectidae	0	27 (16/0)	5 (4/0)	32 (20)
Bathylagus ochotensis	Bathylagidae	0	21 (13/0)	10 (4/4)	31 (21)
Parophrys vetulus	Pleuronectidae	0	19 (9/0)	7 (5/0)	26 (14)
Cataetyx rubrirostris	Bythitidae	0	20 (12/0)	4 (3/0)	24 (15/0)
Argentina sialis	Argentinidae	0	9 (8/0)	8 (6/0)	17 (14)
Protomyctophum crockeri	Myctophidae	0	1 (1/0)	10 (4/4)	11 (9)
Argyropelecus spp.	Sternoptychidae	0	0	9 (4/0)	9 (4)
Pleuronichthys spp.	Pleuronectidae	0	6 (3/0)	3 (3/0)	9 (6)
Ophidion scrippsae	Ophidiidae	0	1 (1/0)	6 (3/0)	7 (4)
Atractoscion nobilis	Sciaenidae	0	6 (2/0)	0	6 (2)
Neoclinus stephensae	Chaenopsidae	6 (2/0)	0	0	6 (2)
Hypsoblennius spp.	Blenniidae	3 (2/0)	2 (2/0)	0	5 (4)
Pleuronichthys coenosus	Pleuronectidae	4 (3/1)	1 (1/0)	0	5 (5)
Coryphopterus nicholsii	Gobiidae	0	4 (3/0)	0	4 (3)
Scorpaenichthys marmoratus	Cottidae	4 (2/0)	0	0	4 (2)
Triphoturus mexicanus	Myctophidae	0	1 (1/0)	3 (2/0)	4 (3)
Bathylagus wesethi	Bathylagidae	0	3 (2/0)	0	3 (2)
Chauliodus macouni	Chauliodontidae	0	0	3 (2/1)	3 (3)
Hypsopsetta guttulata	Pleuronectidae	0	3 (3/0)	0	3 (3)
Lampanyctus spp.	Myctophidae	0	1 (1/0)	2 (1/1)	3 (3)
Oxyjulis californica	Labridae	0	3 (2/0)	0	3 (2)
Tarletonbeania crenularis	Myctophidae	0	2 (2/0)	1 (1/0)	3 (3)
Zaniolepis frenata	Hexagrammidae	0	2 (2/0)	1 (1/0)	3 (3)
Girella nigricans	Kyphosidae	0	2 (2/0)	0	2 (2)
Pleuronichthys ritteri	Pleuronectidae	0	2 (1/1)	0	2 (2)
Tactostoma macropus	Melanostomiidae	0	0	2 (1/0)	2 (1)
Bathylagus milleri	Bathylagidae	0	1 (1/0)	0	1 (1)
Brosmophysis marginata	Bythitidae	0	1 (1/0)	0	1 (1)
Chilara taylori	Ophidiidae	0	1 (0/1)	0	1 (1)
Cololabis saira	Scomberesocidae	1 (0/1)	0	0	1 (1)
Hypsoblennius gentilis	Blenniidae	1 (1/0)	0	0	1 (1)
Hypsoblennius jenkinsi	Blenniidae	1 (1/0)	0	0	1 (1)
Lampanyctus ritteri	Myctophidae	0	1 (0/1)	0	1 (1)
Melamphaes sp.	Melamphaidae	0	1 (1/0)	0	1 (1)
Scomber japonicus	Scombridae	0	1 (1/0)	0	1 (1)
Trachipterus altivelis	Trachipteridae	0	1 (1/0)	0	1 (1)
Typhlogobius californiensis	Gobiidae	1 (1/0)	0	0	1 (1)

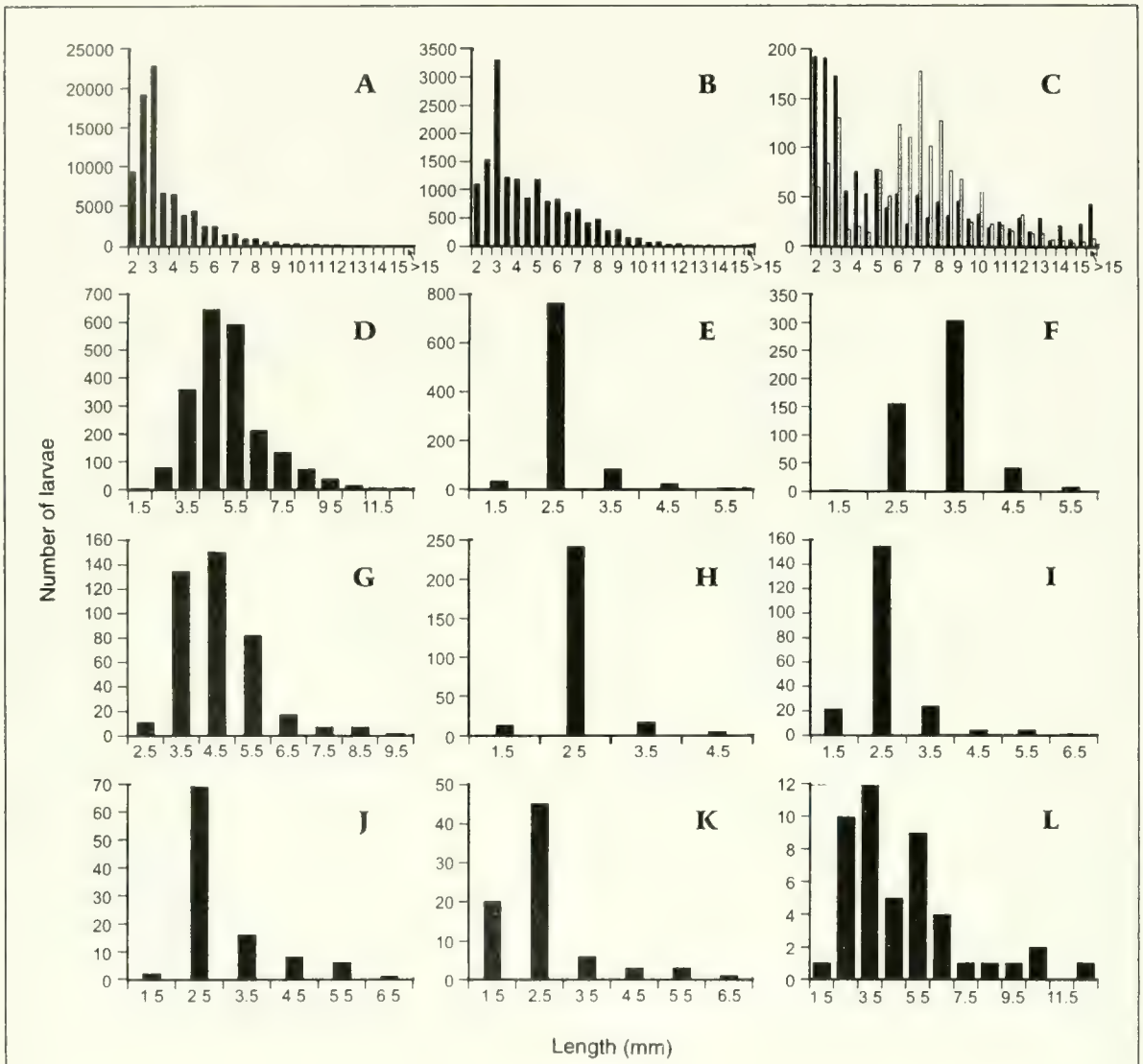

Figure 10

Length frequencies of larvae of the 10 most abundant taxa taken in MESSHAI (**A** and **D–L**), (**B**) oblique bongo, and (**C**) Manta tows on Cruise 8003-EB. (**A–C**) *Engraulis mordax*; day (shaded) and night (solid) are shown for Manta tows; (**D**) *Leuroglossus stilbius*; (**E**) *Genyonemus lineatus*; (**F**) *Stenobrachius leucopsarus*; (**G**) *Sebastes* spp.; (**H**) *Seriphus politus*; (**I**) *Peprilus simillimus*; (**J**) *Paralichthys californicus*; (**K**) *Citharichthys* spp.; (**L**) *Merluccius productus*. In A–C, bars represent 0.5-mm size classes; in D–L, bars represent the midpoints of 1.0-mm size classes.

poststorm samples from the surface to 30 m (Fig. 13, E and F). Individual tows showed a sharp increase in larval density immediately following the storm, peaking 2 days after the storm and declining to prestorm levels 3 days after the storm (Fig. 13, C and D).

***Stenobrachius leucopsarus* larvae** Larvae of northern lampfish occurred throughout the water column to 200 m depth at the inshore station, with highest average densities in the 20–30 m and 30–40 m strata (Fig. 14, A and B). Average densities were greater at the inshore station than at the offshore station. In deep MESSHAI tows taken at the offshore station, average density was greatest in the 40–80 m stratum; larvae were absent between 80 and 160 m. At the inshore station, maximum prestorm larval densities were in the 0–40 m and 40–80 m strata; in poststorm samples, densities were highest at 0–40 m (Fig. 14E). The center of distribution of larval densities from shallow MESSHAI tows shifted upward from 30–40 m in prestorm samples to 20–30 m in poststorm samples (Fig. 14F). Individual deep

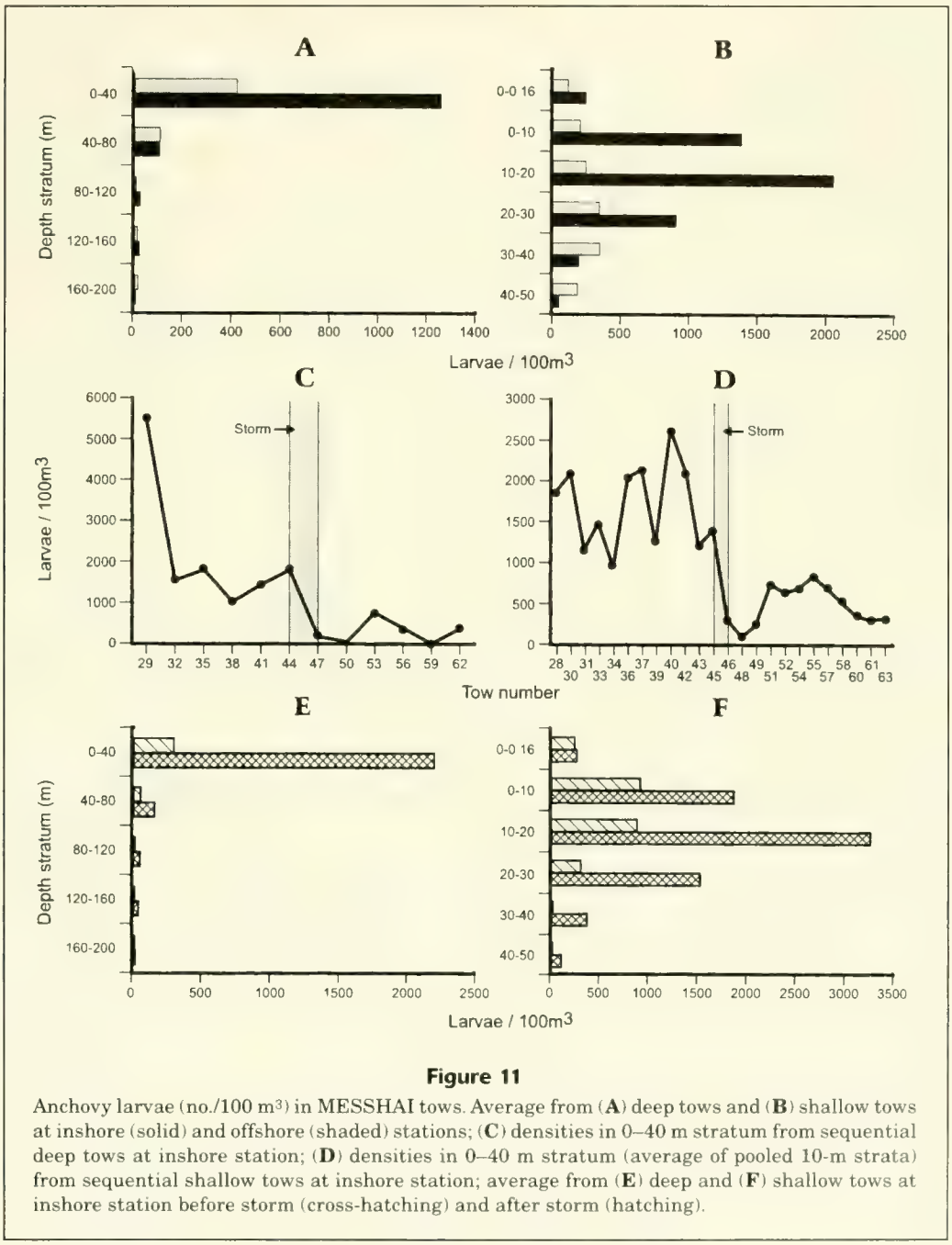

Figure 11

Anchovy larvae (no./100 m^3) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

MESSHAI tows in the upper 200 m showed a trend of increasing density just before the storm and a sharp decrease in poststorm tows (Fig. 14C). In shallow MESSHAI tows, densities peaked in two tows taken one day before the storm but were not appreciably different in pre- and poststorm samples (Fig. 14D).

***Sebastes* spp. larvae** Rockfish larvae were concentrated in the upper 80 m of the water column, with low average densities between 80 and 200 m (Fig. 15A). In deep MESSHAI tows the highest average density was in the 40–80 m stratum at the offshore station but in the 0–40 m stratum at the inshore station (Fig. 15A). In shallow MESSHAI tows at the inshore station, average density was highest in the 20–30 m stratum, relatively low in the 0–10 m and 10–20 m strata, and nearly as high at the surface as in the 20–30 m stratum. Offshore, shallow MESSHAI tows showed extremely low average densities in the upper 30 m of the water column; larvae were not taken in surface net tows. At the inshore station, average larval densities were higher in samples

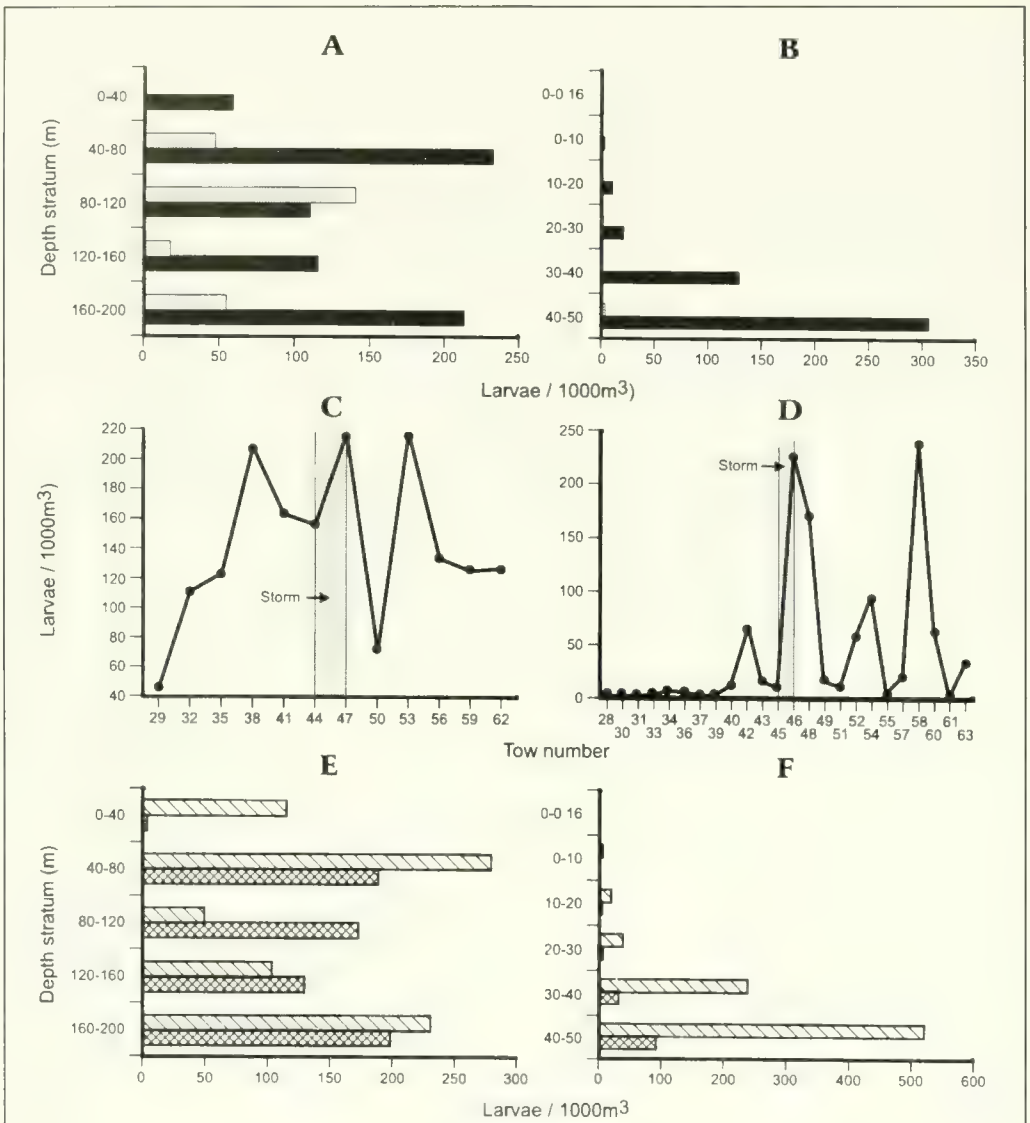

Figure 12

Leuroglossus stilbius larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

taken before the storm than those taken afterwards; however, the disparity between average densities before and after the storm was due largely to several prestorm tows with unusually high larval counts (Fig. 15, C–F).

***Seriphus politus* larvae** Queenfish larvae occurred only at the inshore station, primarily in the upper 10 m of the water column (Fig. 16, A and B). At the inshore station, larvae were virtually absent from tows taken before the storm; larval density increased abruptly immediately following the storm, then subsided to prestorm level within about two days after the storm (Fig. 16, C–F).

***Peprilus simillimus* larvae** Larval Pacific pompano occurred primarily in the upper 40 m, with highest average densities in the upper 20 m of the water column (Fig. 17, A and B). Except for two tows at the 30–40 m stratum, larvae did not occur in offshore

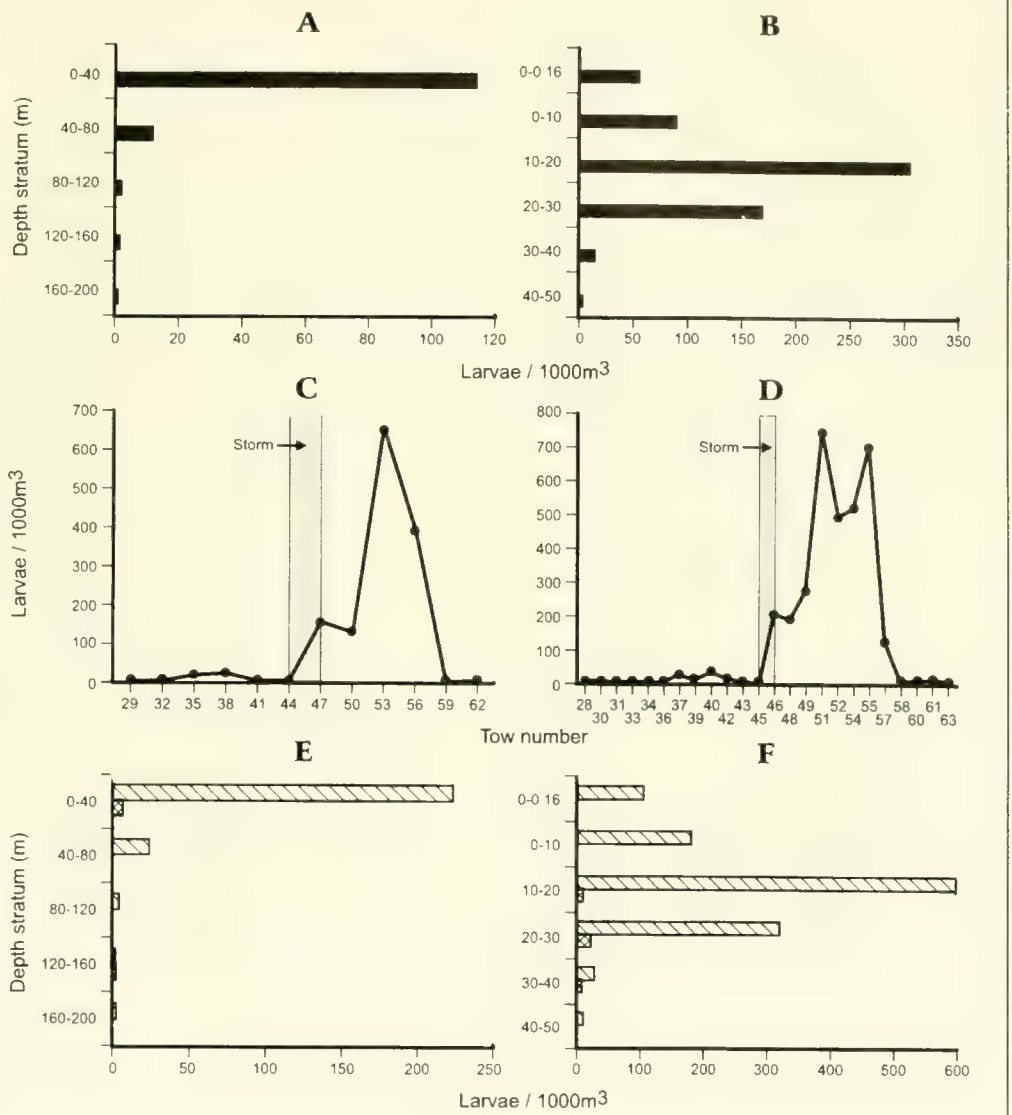

Figure 13

Genyonemus lineatus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

samples. At the inshore station, larval densities were comparatively low in prestorm samples but increased markedly after the storm (Fig. 17, C–F).

***Paralichthys californicus* larvae** California halibut larvae occurred only at the inshore station and were restricted to the upper 30 m of the water column (Fig. 18, A and B). Average larval density was highest in the 0–10 m stratum, where it was four times higher than in the 20–30 m stratum or at the surface (Fig. 18B). Larvae appeared in several of the shallow MESSHAI tows prior to the storm at densities as high as approximately 20 per 1000 m^3; after the storm, densities increased steadily to more than 60 per 1000 m^3, then decreased to prestorm levels within 2 days following the storm (Fig. 18D). Average poststorm larval density for the 10-m stratum was more than 7 times higher than prestorm density, and overall vertical distribution was slightly shallower in poststorm samples (Fig. 18F). Larvae occurred in Manta net samples only in poststorm tows.

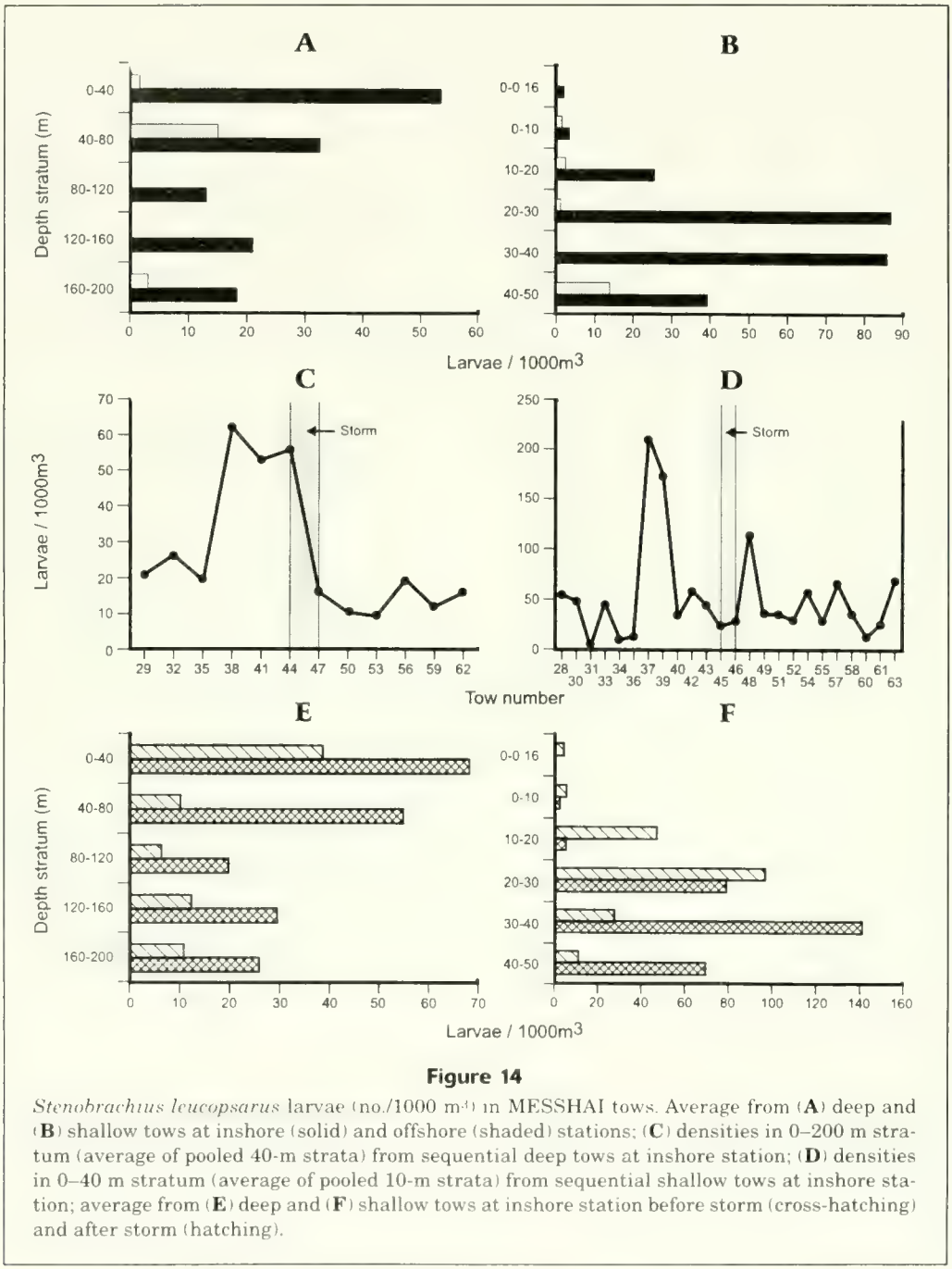

Figure 14

Stenobrachius leucopsarus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

***Citharichthys* spp. larvae** Sanddab larvae were taken primarily in the upper 50 m of the water column at the inshore station (Fig. 19, A and B). In shallow MESSHAI tows, peak average density was in the upper 10 m. Poststorm samples contributed most of the larvae (Fig. 19, C–F). A few larvae appeared sporadically in tows taken before the storm; following the storm there was a steady increase in larval density and then a sharp decline by the second day after the storm (Fig. 19, C and D). The distribution was shifted upward by approximately 20 m in poststorm samples (Fig. 19F).

***Merluccius productus* larvae** Hake larvae were taken in deep MESSHAI tows in the 40–80 and 80–120 m strata; average densities were similar in inshore and offshore samples (Fig. 20A). Larvae occurred in shallow MESSHAI tows only at the inshore station and were taken as shallow as 10–20 m (Fig. 20B). After the storm only one deep MESSHAI tow was positive, but for shal-

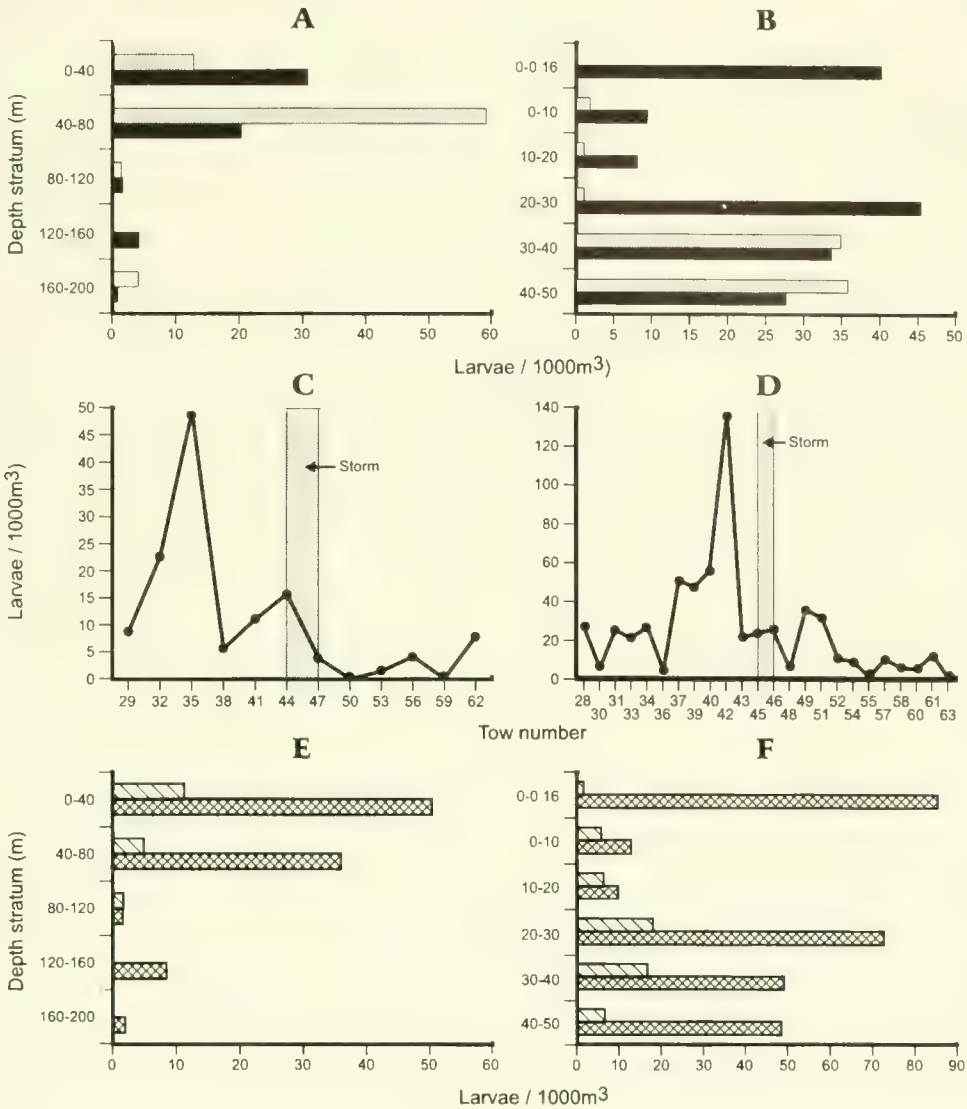

Figure 15

Sebastes spp. larvae (no./1000 m³) in MESSHAI tows. Average of (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

low MESSHAI tows, the frequency of positive tows increased, along with larval densities (Fig. 20, C and D). The distribution of larvae became somewhat shallower in shallow MESSHAI tows after the storm (Fig. 20F).

Discussion

Northern anchovy larvae dominated samples from both study sites. The midwater species *Leuroglossus stilbius* and *Stenobrachius leucopsarus* and the rockfish genus *Sebastes* were relatively abundant at the two sites. These three taxa, along with *Merluccius productus* (ranked 10th in abundance) and *Bathylagus ochotensis* (ranked 13th), constitute a distinct larval recurrent group in the California Current region (Moser and Smith, 1993). These three taxa were also closely linked in other analyses of larval fish assemblages in the study region (Gruber et al., 1982; McGowen, 1993). *Sebastes* spp. and *Merluccius*

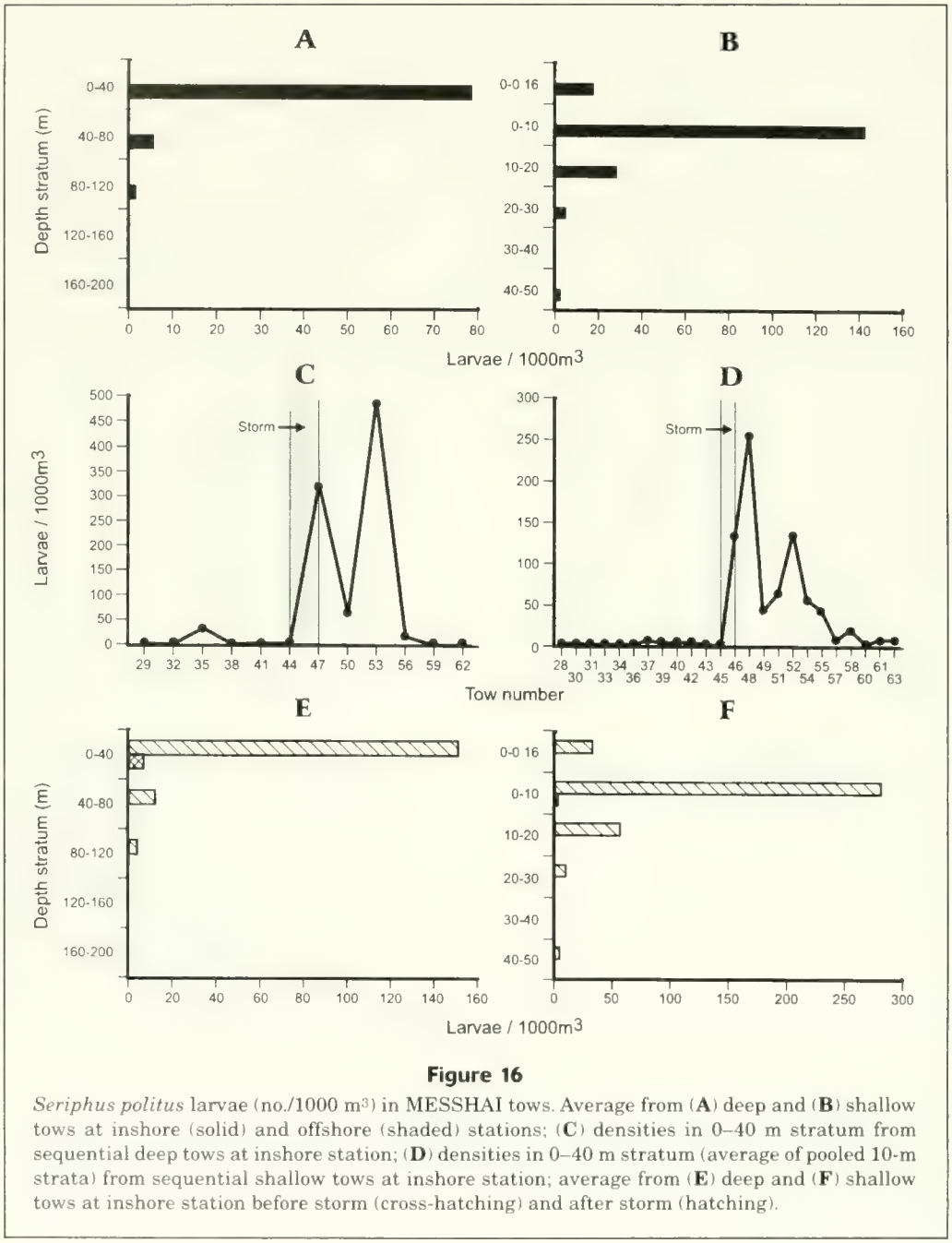

Figure 16

Seriphus politus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

productus are demersal and their larvae are found throughout the SCB at this season (Moser et al., 1993). Other studies (Gruber et al., 1982; McGowen, 1993) have shown that larvae of *Leuroglossus stilbius* and *Stenobrachius leucopsarus* are relatively abundant nearshore and, according to Barnett et al. (1984), *S. leucopsarus* may extend shoreward to midshelf. This can be explained, in part, by the narrowness of the shelf in this region and the proximity to deep-water habitat. These species are unusual in comparison with other bathylagids and myctophids in this region in having relatively high larval abundances near the coast (Moser et al., 1993). Most larvae of other taxa collected in this study were taken at the nearshore station and represent demersal shelf species. The most abundant of these, *Genyonemus lineatus*, spawns during winter and early spring over shelf waters throughout the SCB (Gruber et al., 1982; Schlotterbeck and Connally, 1982; Watson, 1982; Barnett et al., 1984; Brewer and Kleppel, 1986; Lavenberg et al., 1986; Walker et al., 1987; McGowen, 1993; Moser et al., 1993). *Seriphus politus*, the next

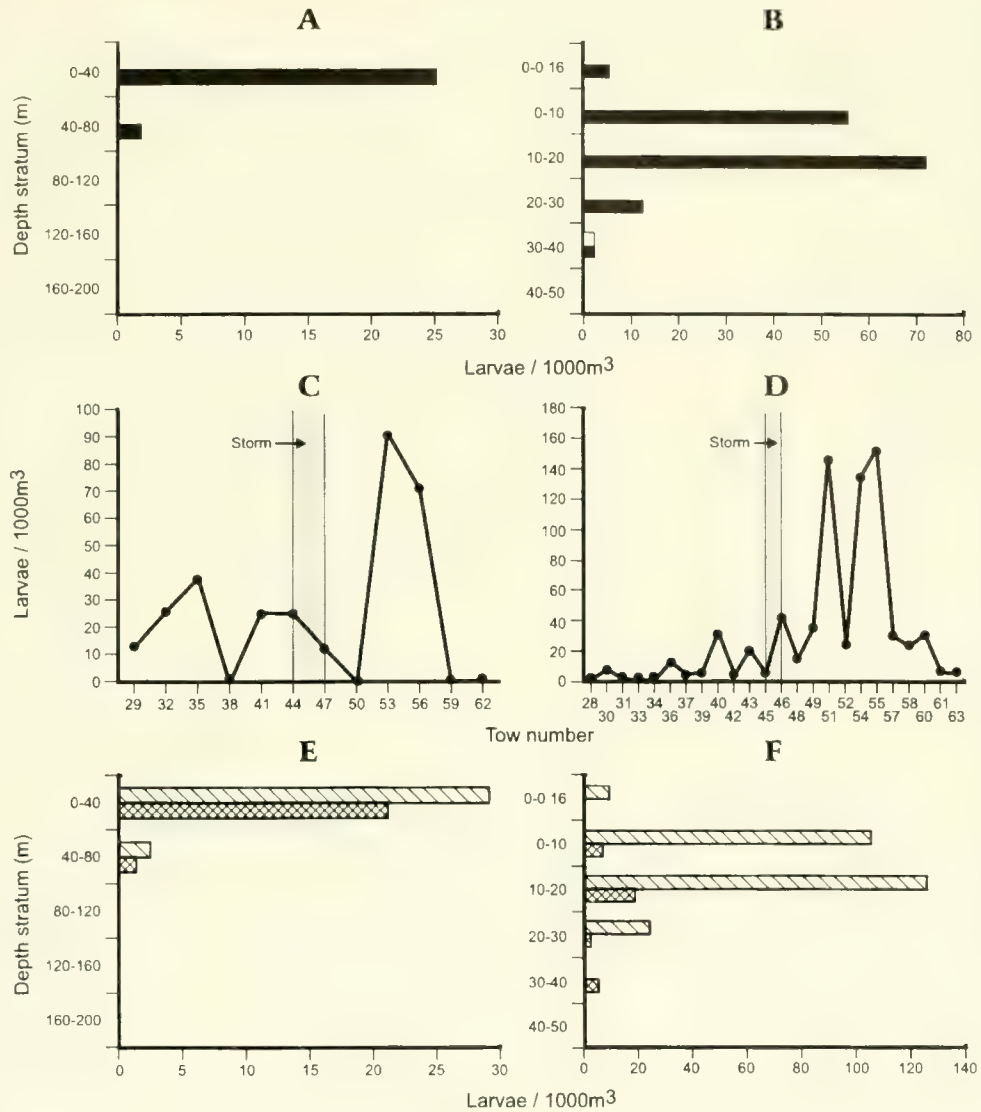

Figure 17

Peprilus simillimus larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

most abundant shelf species in the samples, typically spawns from late spring to summer; however, spawning began unusually early in 1980 since larvae were abundant as early as March off San Onofre (Walker et al., 1987). *Peprilus simillimus*, *Paralichthys californicus*, and *Citharichthys* spp. have broad spawning seasons with high larval abundance in late winter to early spring. This was particularly evident in 1980 (Walker et al., 1987; Moser et al., 1993).

The vertical distribution of larval fishes is closely related to the temperature profile of the water column. Ahlstrom (1959) described two general categories: those taxa whose larvae occur almost entirely within the upper mixed layer and in the upper part of the thermocline; and those that occur within or below the thermocline. Larvae of shorefishes, including most clupeoids, typically fall within the first category. Generally, slope and offshore taxa produce deeper-living larvae, although many oceanic taxa also have shallow-living larvae. Northern anchovy had similar vertical profiles at the slope and offshore stations although densities were much higher at the slope station, where the

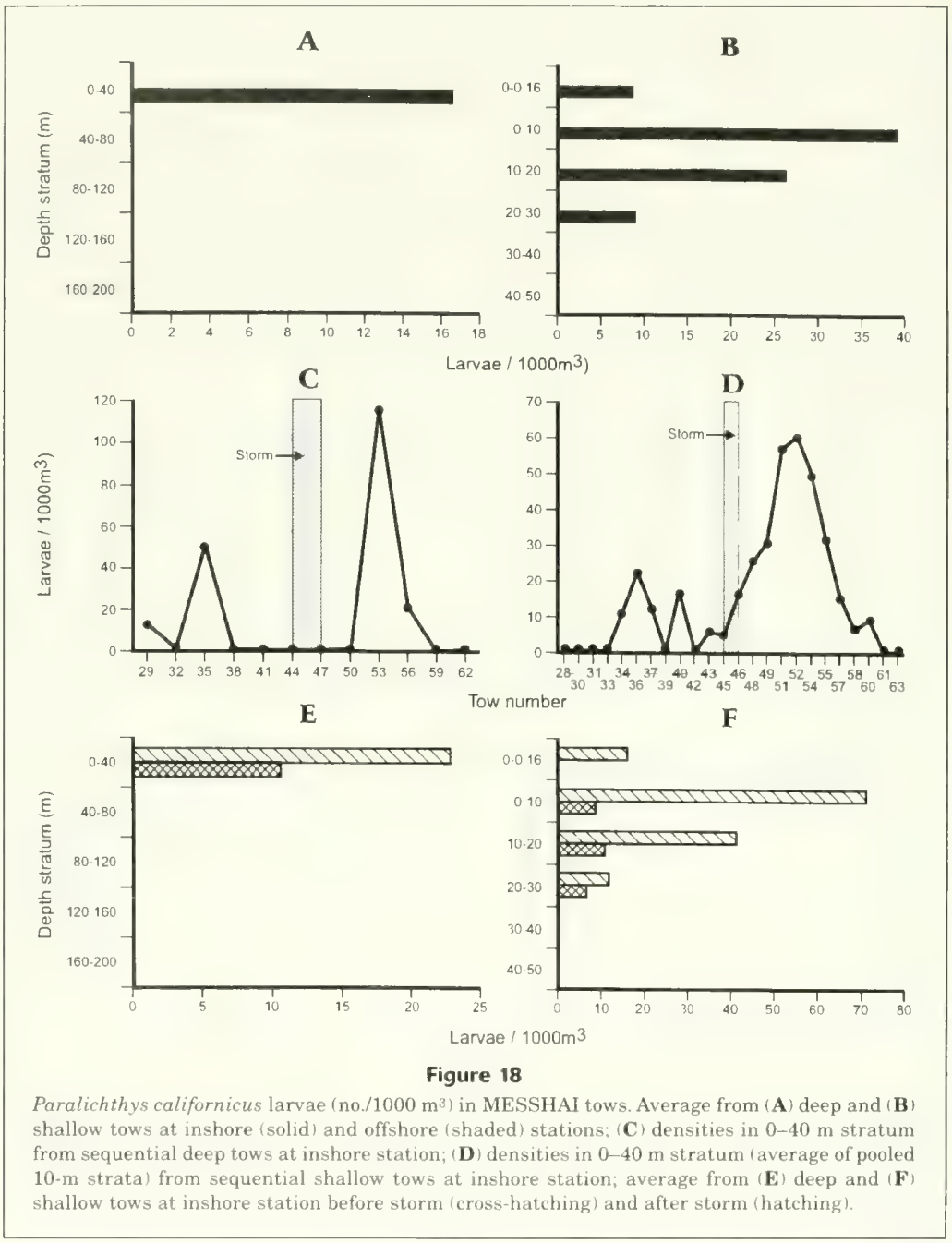

Figure 18

Paralichthys californicus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

density peak was more pronounced and was about 10 m shallower than at the offshore station. Probably this peak was related to the relatively shallow mixed layer at the slope station compared with the offshore station. Eggs of the anchovy had a shallower distribution than the larvae, with an apparent density peak in the neuston. The effect of the different mixed layer depths at the two stations is evident in the slightly deeper lower distribution boundary of eggs at the offshore station.

Like the anchovy, the nearshore shelf species (white croaker, queenfish, California halibut, California pompano, and some sanddab species) had shallow larval distributions essentially limited to the upper 30 m of the water column of the inshore station, with peak densities in either the 0–10 m or 10–20 m strata. Such shallow distributions appear to be typical of nearshore species although previous studies have lacked the fine-scale sampling capability needed to show this. The many *Sebastes* species occupy a wide range of habitats on the shelf and upper slope and produce larvae that are found within and below the thermocline and that generally avoid the upper mixed layer, except for the

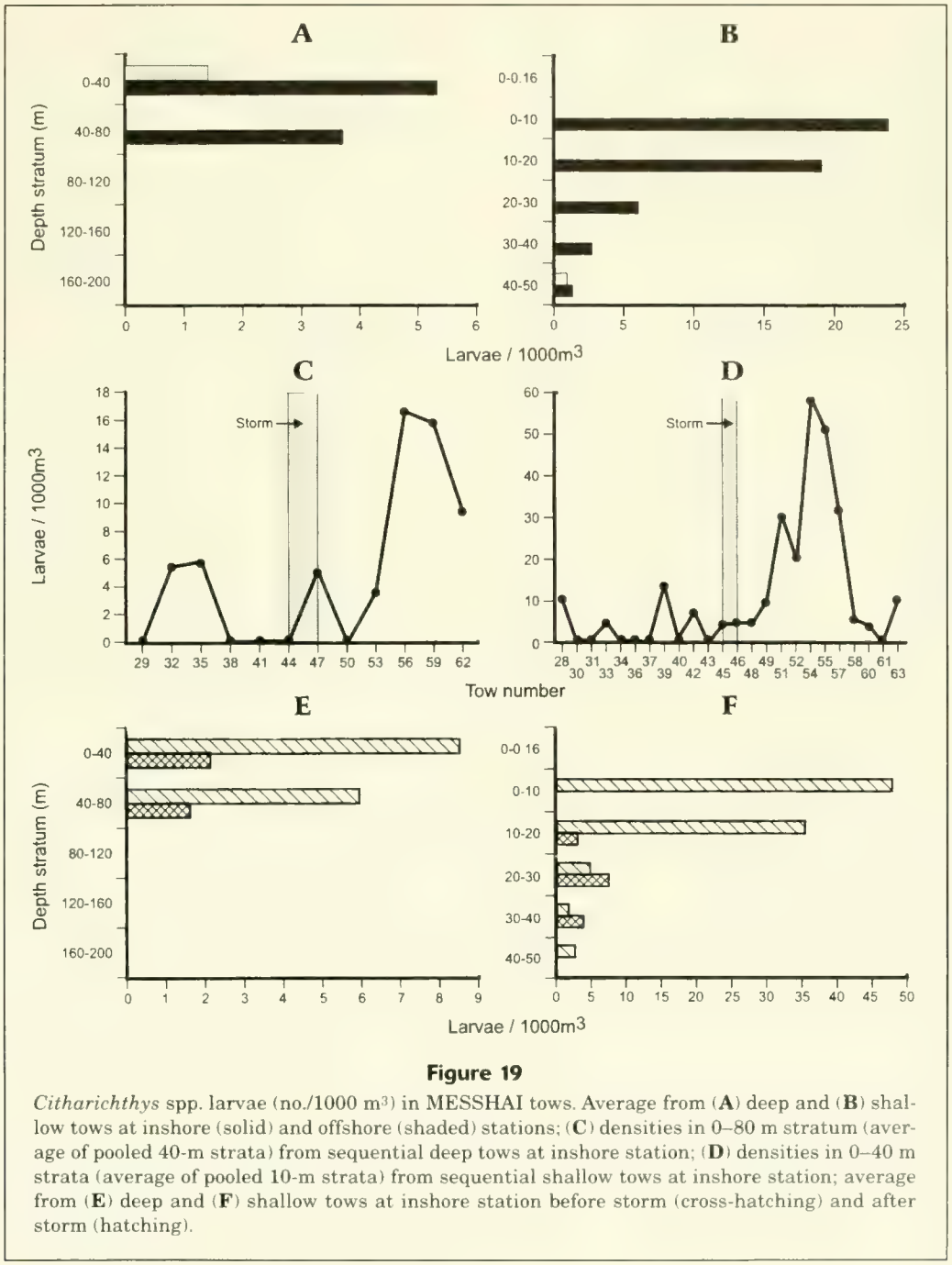

Figure 19

Citharichthys spp. larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–80 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m strata (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

neustonic zone (Ahlstrom, 1959; Moser and Boehlert, 1991). This distribution is clearly shown by comparing the stratum of highest density at the inshore and offshore stations. Likewise, Pacific hake are broadly distributed over the shelf and slope and have deep-living larvae (Ahlstrom, 1959; Mullin and Cass-Calay, 1997). In our study, hake larvae were absent from samples above 50 m depth at the offshore station.

A comparison of larval anchovy length distributions from MESSHAI, bongo, and Manta net tows shows that the MESSHAI is less effective in catching larvae over 3 mm than the other two (Fig. 10, A–C). The mouth opening of the MESSHAI net is relatively much smaller (25×25 cm) than that of the bongo net (71 cm diameter). Why the Manta net captures larger larvae is conjectural. It may be related to the absence of an upward escape plane for larvae in the path of the net or it may reflect the size frequency of larvae in the surface layer. The bimodal length distribution for anchovy captured in Manta

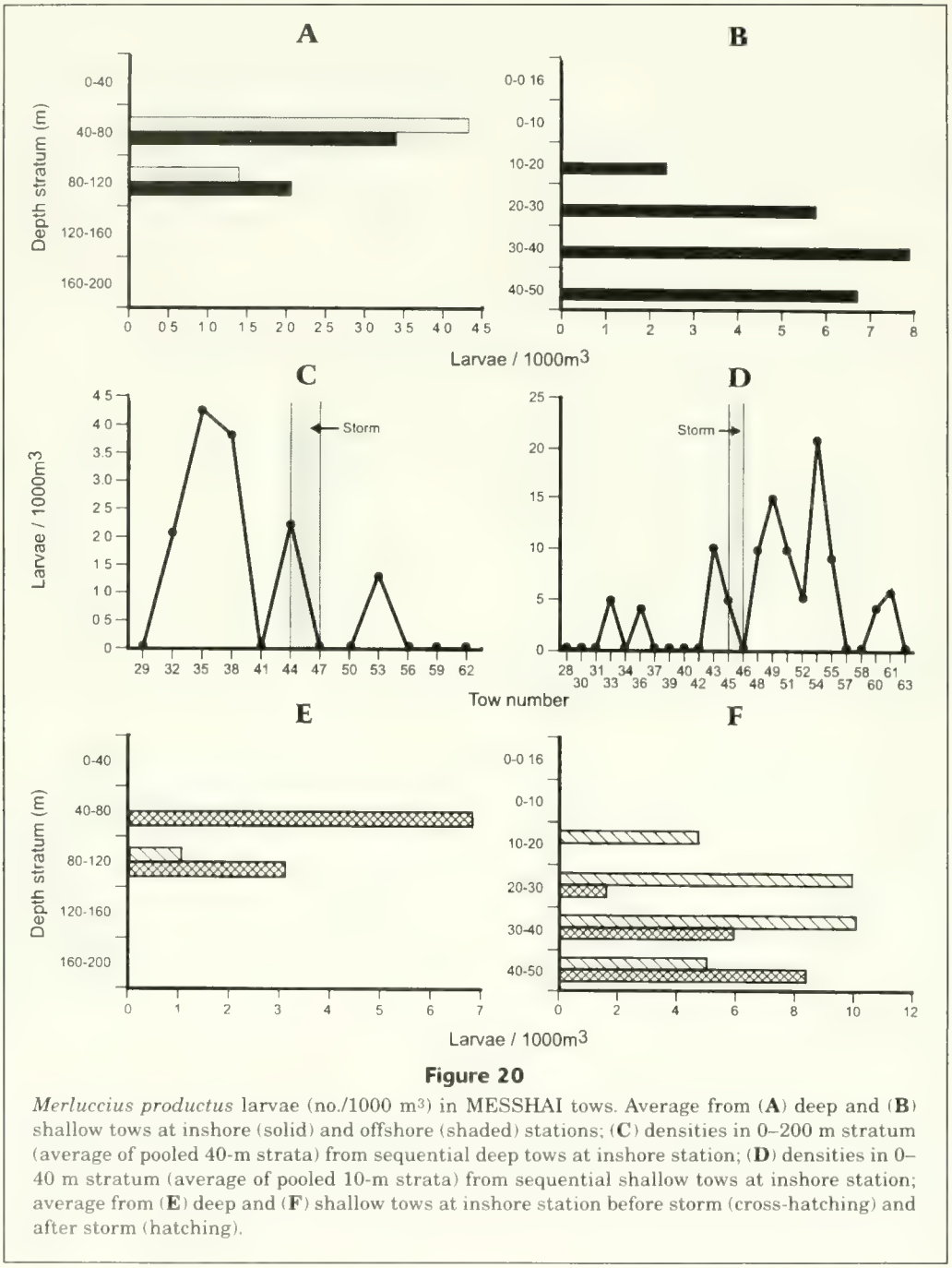

Figure 20

Merluccius productus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

tows results from relatively large numbers of 6.0–10.0 mm larvae caught at the surface during the day (Fig. 10C). This was a consistent feature of Manta catches throughout the cruise, suggesting that anchovy larvae may have been migrating to the surface layer to feed during the day.

The storm that interrupted sampling for two days at the inshore station significantly affected the relative abundance and distribution of fish larvae and their physical and biotic environment. Average densities of anchovy larvae declined markedly in most strata following the storm, possibly as a result of mortality associated with starvation. This argument is contradicted by the results of Mullin et al. (1985) who showed that important larval fish prey, such as copepod nauplii increased in concentration after the storm, were no less stratified than before the storm, and had a 15-m upward shift in peak abundance that mirrored the shoaling of anchovy larval distribution in our study. Moreover, the chlorophyll maximum was

below the peak depth zone of anchovy larval abundance before the storm, whereas it coincided with the depth zone of highest larval abundance afterwards. Pre- and poststorm peak concentrations of important fish larva prey coincided with pre- and poststorm peaks in the chlorophyll maximum (Mullin et al., 1985). If starvation was the reason for the decline in anchovy larvae, then it is likely that the cause was disruption of micropatches of food, as suggested by Mullin et al. (1985). In this case, Lasker's (1981) stable ocean hypothesis was operative at the centimeter scale, and reduced survival was a result of disruption of the fine-scale geometry of food patches (Vlymen, 1977; Owen, 1989). Another explanation for the poststorm decline in anchovy larval abundance would be advection of larvae away from the study site (Mullin et al., 1985). The strong northwest winds resulted in offshore movement of surface water (the upper 10 m) by Ekman transport at a rate of about 10 cm per second; thus, virtually all the surface water at this region of the shelf was moved offshore during the storm and was replaced by deeper water (Winant[1]). This could explain the sharp decline in anchovy larval densities at the slope station after the storm, providing, of course, that densities of anchovy larvae were lower over the shelf than at the station before the storm. The latter would not be expected since Barnett et al. (1984) showed high concentrations of anchovy larvae over the shelf at a similar habitat south of our inshore station.

The storm had an opposite effect on densities of shorefish larvae (*Genyonemus lineatus, Seriphus politus, Peprilus simillimus, Paralichthys californicus, Citharichthys* spp.), which occurred in extremely low densities or which were absent in prestorm samples. Larval densities of these species began to increase immediately after the storm, peaked within 1–2 days, and then declined abruptly to prestorm levels. The sudden appearance of these larvae at the nearshore station after the storm was a result of storm-induced advection from shallow regions of the shelf. The narrow shelf in this region of the coast would make nearshore fish larvae particularly vulnerable to transport off the shelf during storms with northwest winds. Such advection may be important in the transport of nearshore fish larvae seaward where they become available to slope or eddy circulation, thus providing the opportunity for dispersion to other regions. The subsequent rapid decline in larval densities could have been caused by mortality associated with disturbance of micropatches of food, by predation, or by active or passive movement of larvae away from the sampling site. Starvation of these inshore larvae over slope waters may be related to the difference in composition and concentration of prey organisms in nearshore and offshore waters (Watson and Davis, 1989). Some portion of the larvae that appeared at the inshore site after the storm may have been transported back to the nearshore region. This return transport may have been enhanced by upward movement of these larvae to the surface where they could be carried by shoreward currents created by internal wave cells (Shanks, 1983, 1986).

Among the species with deeper-living larvae, those of *Sebastes* spp. declined markedly in all strata after the storm, whereas those of *Stenobrachius leucopsarus* showed a decline in deeper strata but increased in strata shallower than 30 m. This probably was caused by upward turbulent advection of larvae from deeper strata. Likewise, larval density of *Leuroglossus stilbius* increased in strata shallower than 50 m following the storm, with sporadic high counts in individual tows, suggesting pulses of upwardly advected larvae.

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[1] C. D. Winant. 1998. Center for Coastal Studies, Scripps Institution of Oceanography, La Jolla, CA 92093. Personal commun.

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Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging

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Abstract.—Growth parameter estimates were calculated for the tiger shark (*Galeocerdo cuvier*) by using tag and recapture data. Results were compared to published estimates based on bands in vertebrae. The von Bertalanffy parameters (sexes combined) based on tag and recapture growth data were as follows: L_∞ = 337 cm fork length, k = 0.178, and t_0 = −1.12. Monthly length-frequency data for six year classes from birth to two years old for tiger sharks were used to verify the tag-recapture growth curve for this age range. The predicted age at maturity is 7 years for both sexes. Data from an ongoing *in situ* study with oxytetracycline were used in conjunction with length data to determine the effect of tagging and oxytetracycline injection on growth. The data suggest that tagging alone or tagging combined with oxytetracycline injection has little or no effect on the growth rate of tiger sharks up to two years of age.

Adult tiger sharks, *Galeocerdo cuvier*, occur worldwide in temperate and tropical coastal waters. In the North Atlantic, they reside year round off the coast of Florida and seasonally migrate north as far as Nova Scotia, Canada (Kohler et al., 1995). Additionally, tiger sharks are known to make extensive migrations throughout the North Atlantic, on occasion traveling to Cuba and Africa.[1] The tiger shark is listed under the large coastal shark category of the Fisheries Management Plan for Sharks of the Atlantic Ocean (Anonymous, 1993). Although it is not a target species of the U.S. inshore longline fishery, small tiger sharks are frequently caught and released alive. Tagging and fishery data indicate that there is a nursery ground for tiger sharks on the continental shelf off the southeast coast of the US.[1] This area extends from about Augusta, GA, to Daytona, FL, and extends from shore seaward to depths of 100 m. A similar area exists off the coast of North Carolina.[2] In these areas, tiger sharks of birth size ranging from 61 cm fork length [FL]) to 120 cm FL are commonly caught in the commercial longline fishery. In the Northwest Atlantic, tiger sharks mature between 258 and 265 cm FL (Branstetter et al., 1987) and have been reported to attain a size of 469 cm FL (Castro, 1983).

Branstetter et al. (1987) used the alternating opaque and translucent bands formed in the vertebral centra to age tiger sharks caught in the western North Atlantic and the Gulf of Mexico. Attempts to verify these estimates with length-frequency analysis proved unsuccessful owing to the inability to distinguish age groups. Branstetter et al. (1987) tried to corroborate the vertebrally derived growth rate with results from one tag-recapture individual; however, this individual's length was estimated at both tagging and recapture. Owing to the high age estimates at L_∞, Branstetter et al. (1987) suggested that as tiger

[1] 1992–98. Apex Predators Program, 28 Tarzwell Dr. Narragansett, RI 02882. NMFS unpub. data.

[2] Chris Jensen. 1994. Natl. Mar. Fish. Serv, NOAA, 28 Tarzwell Dr., Narragansett, RI 02882. Personal Commun.

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sharks approach maximum sizes, their vertebrae and band deposition may not reflect age. Because attempts at verification were unsuccessful, and direct validation was not possible, the determination of the tiger shark growth rate was not completely satisfied.

To determine if vertebral growth bands reflect age in older individuals and possibly to verify the estimates of Branstetter et al. (1987), we undertook a study with tag and recapture data to estimate, independently, von Bertalanffy parameters for the tiger shark. Verification of neonatal and juvenile growth rates was accomplished by using monthly length-frequency data obtained over a period of seven years. In addtion, data on growth of oxytetracycline (OTC)-injected tagged and released tiger sharks from an ongoing study were available to compare with length-frequency and tagging growth data.

Figure 1

Map showing the portion of the nursery area (shaded box) from which monthly length-frequency samples were obtained.

Materials and methods

Data from tiger sharks were obtained between 1963 and 1997 from research vessel cruises, sportfishing tournaments, and the commercial shark fishery from Cape Cod, MA, to the Florida east coast. Data for monthly length-frequency analyses were obtained from tiger sharks caught by longline in a delineated area within the nursery grounds off Florida during 1988–94 (Fig. 1).

Length measurements

Measurements of total length (TL) and FL were taken to the nearest centimeter (cm) following the conventions of Bigelow and Schroeder (1948). Fork lengths are reported unless otherwise noted. TL to FL conversions can be calculated from the relationship

$$FL = (TL \times 0.8761) - 13.3535 \qquad r^2 = 0.99 \; n=44$$

(Kohler et al., 1995)

Tag-recapture data

During 1962–96, over 6000 tiger sharks were tagged with NMFS tags (Casey, 1985) and released as part of the NMFS Cooperative Shark Tagging Program. Tags were returned primarily by sport and commercial fishermen who also reported shark size in TL, FL, or weight. All measurements and estimates were converted to FL.

Gulland and Holt's (1959) and Fabens' (1965) methods were used to calculate von Bertalanffy (1938) growth parameters from the tag-recapture data. Techniques for calculating the parameters according to Gulland and Holt (1959) came primarily from their publication and additional clarification was obtained from Cailliet et al. (1992). Only fish that were measured at both release and recapture and at liberty for at least 0.9 years were included in the analysis. Two of the three parameters for the von Bertalanffy (1938) growth function (VBGF), k and L_∞, were estimated directly with the methods of Fabens (1965) and Gulland and Holt (1959). T_0 cannot be estimated from tagging data alone, rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF and solving for t_0, such that

$$t_0 = t + (1/k)\left[\ln\left\{(L_\infty - L_t)/L_\infty\right\}\right],$$

where L_t = known length at age (size at birth);
k = the von Bertalanffy growth constant; and
L_∞ = the theoretical maximum attainable length from the VBGF.

The t_0 values were calculated based on an average size at birth of 61 cm FL[1] with $t = 0$.

Longevity was estimated from the FL at which >99% of the L_∞ was reached (i.e. $7\ln 2/k$) (Fabens, 1965; Cailliet et al., 1992). The von Bertalanffy parameters derived from these methods were compared with growth information obtained from the length-

frequency analysis. No OTC-injected individuals were included in these calculations.

Tag-recapture with OTC injection

During 1985–97, more than 650 tiger sharks (59 to 291 cm FL) were measured, injected with a 25 mg/kg body weight dose of OTC (Gruber and Stout, 1983), tagged, and released. To determine the effects of OTC on growth, data from recaptured OTC-injected fish were analyzed separately from those of noninjected recaptured fish. Only those OTC-injected specimens measured at both tagging and recapture and at liberty for at least 0.9 years were included in the analysis. For comparison of growth of injected fish to growth of noninjected fish, the growth rates from OTC-injected individuals were plotted with the von Bertalanffy growth function (VBGF) from the tag-recapture analysis. The size at tagging was used as a guide to estimate age at tagging with the VBGF. The time at liberty determined the distance along the x-axis, and sizes at recapture determined the slope. The growth of the OTC-injected individuals was then compared graphically with the growth curves for long-term (>0.9 yr) tag-recaptured sharks and monthly growth estimates.

Monthly growth

Data for tiger sharks measured and subsequently tagged from the defined nursery area were analyzed for monthly growth. Data on measured fish were available by month from June 1988 to August 1994. Data were organized into 5-cm intervals. The modes for the 1988, 1989, 1990, 1991, 1992, and 1993 year classes were followed progressively from the birth mode until the last visible mode for that year class. Where modes were not clear (i.e. single fish at more than one interval) the mean was taken as the mode. Previously tagged individuals were not included in this data set. Length-frequency histograms were developed for each month of each year for modal analysis. To determine if the data from the six year classes could be combined, the modes of each year class were plotted by month and compared graphically and through an analysis of covariance. Growth per year was calculated by subtracting the June birth mode from the June one-year mode and the June one-year mode from the June second-year mode. To compare the growth of these fish to tagged noninjected fish and tag-recaptured OTC-injected fish, month-per-year growth rates were plotted against the VBGF from the recapture analysis and the growth rates from the individual tag-recaptured OTC-injected fish. The initial positioning of the modes on the x-axis assumes birth takes place in June[1] so that the first point of the monthly growth was fixed on the monthly tag-recapture curve for June. The monthly growth values were fixed on the curve on the basis of month they were calculated for (i.e. June, birth; June, year 1; June, year 2). Graphical comparisons enabled us to determine whether growth based on the tag-recapture analysis was distinct from growth based on a method without tagging (represented by monthly growth). In addition, we compared Branstetter et al.'s (1987) vertebral growth curve to these data.

Results

Tag-recapture data

Information on 42 recaptured tiger sharks, measured at both tagging and recapture and at liberty for at least 0.9 years, was used to produce values of L_∞ and k of the VBGF (Table 1). The Gulland and Holt (1959) method produced the most biologically plausible estimates of VBGF parameters (Table 2). The Fabens (1965) analysis underestimated L_∞ with known maximum size estimates, and the value for k was high. Therefore, further analysis was based on the results from the method of Gulland and Holt (1959). Age at maturity, based on lengths at maturity from Branstetter et al. (1987), for female (265 cm FL) and male (258 cm FL) tiger sharks is 7 years (Fig. 2; Table 3). Maximum age was estimated to be 27.3 years (335+ cm FL > 99% of L_∞).

Tag-recapture with OTC injection

Analysis of the growth of the four OTC-injected specimens recaptured >0.9 years after tagging indicates that individuals grew at approximately the same rate as predicted by the tag-recapture data (Fig. 3). Growth calculated for the first year (growth/year of two individuals tagged at <100 cm FL) was 42.3 and 48.4 cm/yr. and 39.4 and 48.7 cm/yr. for the second year (growth/year two individuals tagged at >100 cm FL) (Table 1). These four individuals were at liberty between 0.94 and 1.19 years.

Monthly growth

Modes were clearly visible in the length-frequency histograms for small tiger sharks of all year classes from birth to 1.5 years. The modes for 1.5–2 years were less distinct owing to decreased sample sizes at the larger sizes (Fig. 4). Differences in growth rates among the six year classes were statistically significant (ANCOVA, $P>0.05$) so we did not combine the monthly length frequencies for all years (Fig. 4). In

the first year, the young grew from an average birth size of 65 cm FL to 100–105 cm FL with a growth rate of 40–45 cm/yr. (Fig. 4). More limited data on second year growth indicated a rate of 35–45 cm/yr. Even with this variation, growth in all years paralleled the tag-recapture growth curve and the individual growth rates of the OTC specimens (Fig. 3).

Discussion

It is evident that traditional methods for aging teleosts do not always work well for sharks. Length-frequency analysis is difficult owing to the slow growth exhibited by most elasmobranch species. Hard part analysis requires validation of the periodicity of band formation, which is often difficult to obtain for shark species. Vertebral age estimates for the sandbar shark, *Carcharhinus plumbeus*, which was one of the six species considered validated, have been revised since Cailliet's (1990) paper by using tag and recapture evidence (Casey and Natanson, 1992). The new data indicate that although the vertebral bands may be formed annually in the young shark, as validated (Branstetter, 1987b), they are not formed annually throughout the life of the shark and, therefore, band counts severely underestimate age. This type of revision highlights the need for validation of all size classes. It is advisable to use several methods for aging to provide verification for the chosen growth curve, particularly if vertebral band counts are used without direct validation.

Tag-recapture data can be a useful tool for age and growth determination if accurate measurements are taken at both tagging and recapture and if individuals are at liberty for a sufficient time for growth to occur. However, problems are associated with this method as well. For example, most length measurements are estimated by recreational and commercial fishermen. For slow growing sharks, it is imperative to obtain accurate length measurements, particularly in large fish. This can prove difficult as well as dangerous at tagging. Therefore, data on large individuals is sometimes lacking and thus will bias results. Additionally, some researchers have shown that tagging with "M" type tags in small sharks, such as the lemon shark, may retard growth (Manire and Gruber, 1991). Analysis of the data can also be problematic. The Fabens (1965) method can lead to biased estimates because its basic premise, that tagged individuals are at large for equal time periods, is often violated with sharks. Estimates from that method lead to low values of L_∞ and high values of k (Chien and Condrey, 1987). The Gulland and Holt (1959) method, which allows for unequal times at liberty,

Table 1

Tag-recapture data used for growth and growth rate analyses. TAL = time at liberty, FLTAG = fork length at tagging, FLCAP = fork length at recapture, b = value calculated from Gulland and Holt (1959). Also shown are the data for the OTC-injected recaptured fish, although they were not included in growth analyses.

Id No.	Sex	TAL (yr)	FLTAG (cm)	FLCAP (cm)	Average growth/yr (cm)	b
1	M	4.02	75.0	222.0	36.5	0.26
2	F	1.39	76.0	122.0	33.1	0.09
3	M	1.69	76.2	111.8	21.0	0.11
4	F	0.90	77.0	124.0	52.3	0.06
5	F	1.42	78.7	114.3	25.1	0.09
6	F	1.75	79.0	136.0	32.5	0.12
7	M	0.97	85.0	130.0	46.6	0.06
8	F	1.60	86.0	171.0	53.0	0.11
9	F	1.22	88.0	128.0	32.8	0.08
10	F	0.91	89.0	120.0	34.0	0.06
11	F	0.92	90.0	155.0	70.9	0.06
12	F	4.90	91.0	211.0	24.5	0.32
13	M	1.00	91.0	122.0	30.9	0.07
14	F	4.90	91.0	211.0	24.5	0.32
15	M	2.04	91.0	168.0	37.7	0.13
16	F	1.03	94.0	136.5	41.2	0.07
17	F	1.60	96.0	157.0	38.1	0.11
18	M	1.01	97.0	147.0	49.5	0.07
19	F	1.51	98.0	154.0	37.0	0.10
20	M	0.97	98.0	142.0	45.4	0.06
21	F	3.28	98.0	195.0	29.6	0.22
22	F	0.95	102.0	157.0	57.9	0.06
23	F	0.90	104.0	124.0	22.1	0.06
24	M	0.99	106.0	156.0	50.4	0.07
25	M	1.00	106.0	160.0	54.2	0.07
26	M	1.37	108.0	147.0	28.4	0.09
27	F	0.97	109.0	160.0	52.6	0.06
28	F	1.07	110.0	173.5	59.6	0.07
29	M	0.94	111.0	156.0	47.9	0.06
30	F	1.56	114.0	155.0	26.2	0.10
31	F	2.20	117.0	184.0	30.5	0.14
32	F	1.69	117.5	175.5	34.3	0.11
33	M	0.90	118.0	152.0	37.7	0.06
34	M	1.48	120.0	167.0	31.8	0.10
35	M	0.91	121.0	161.0	43.9	0.06
36	F	1.37	124.0	173.0	35.7	0.09
37	M	0.91	124.0	137.0	14.2	0.06
38	F	0.93	149.0	164.0	16.2	0.06
39	M	1.16	170.0	193.6	20.3	0.08
40	F	5.28	190.0	235.0	8.5	0.35
41	F	1.20	281.0	288.0	5.8	0.08
42	M	3.33	287.0	317.5	9.2	0.22
218097	F	0.94	104.0	141.0	39.4	
304303	M	0.98	70.5	112.0	42.3	
190804	F	1.19	100.0	158.0	48.7	
204379	M	1.06	93.5	145.0	48.4	

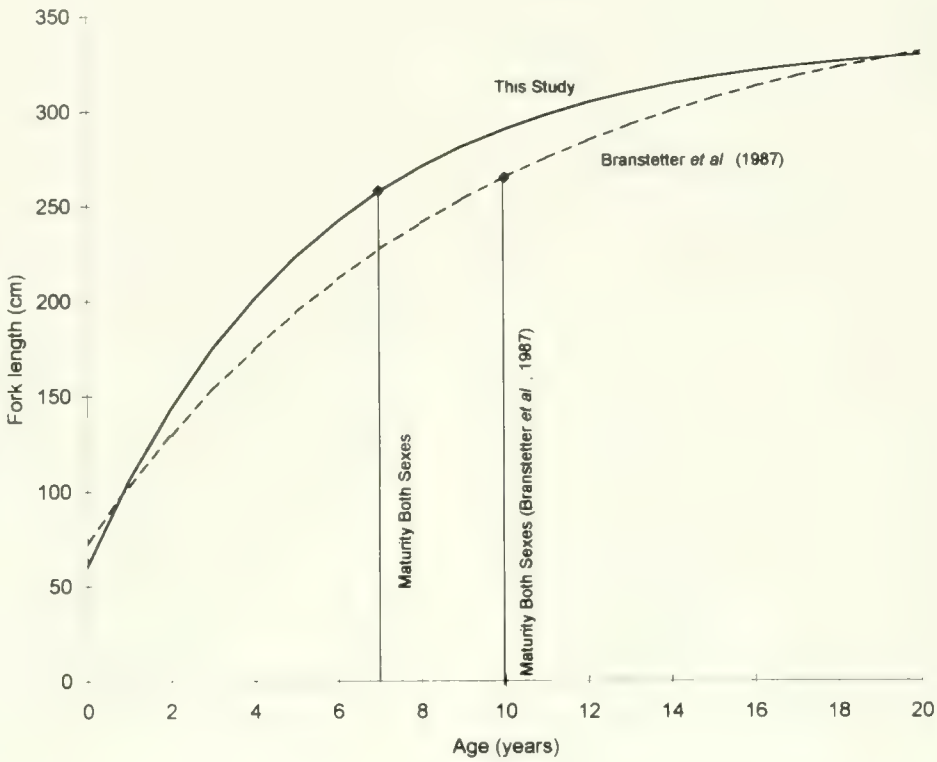

Figure 2

Tag-recapture growth curve derived in this study by using the Gulland and Holt (1959) method compared with the growth curve derived by Branstetter et al.'s (1987) using Atlantic Ocean vertebral data. Estimated size and age at maturity are included on both curves.

Table 2

VBGF parameters calculated by using two different tag-recapture methods (Gulland and Holt, 1959, and Fabens, 1965) (n=42) and compared with Branstetter et al.'s (1987) estimates derived from vertebral analysis (fork lengths calculated by using Branstetter et al.'s (1987) conversions).

Model	L_∞	SE	k	SE	t_0
Gulland and Holt, 1959	337 FL	6.95	0.178	0.048	−1.12
Fabens, 1965	293 FL	19.10	0.217	0.031	−1.08
Branstetter et al., 1987					
Atlantic	440 TL (365 FL)	0.107	−2.35		
Gulf of Mexico	388 TL (324 FL)	0.184	−1.13		

therefore, appears to be more appropriate for sharks (Cailliet et al., 1992).

In this study, the Gulland and Holt (1959) method produced more biologically reasonable results than the Fabens (1965) method. The L_∞ calculated from the Gulland and Holt method was 337 cm FL, which is lower than the maximum reported western North Atlantic values from the literature (391 cm FL; Bigelow and Schroeder, 1948). More recently, in the western North Atlantic and Gulf of Mexico, the largest sharks observed were 346 cm FL (Branstetter, 1981) and 339 cm FL[3] the latter quite close to our

[3] Kohler, N. E., H. W. Pratt Jr., L. J. Natanson, P. Turner, and R. Briggs. 1996. The shark tagger 1995 summary. Narragansett Laboratory, Northeast Fish. Science Center, Natl. Mar. Fish. Serv., NOAA, 16 p.

estimate. However, the tiger shark has been reported to 469 cm FL (Castro, 1983). The L_∞ value estimated from the Fabens (1956) method (293 cm FL), however, is lower than all reported values. In addition, the Fabens (1965) method value for k is high (Table 2). We therefore concluded that the Gulland and Holt (1959) VBGF is the more appropriate model to use for the tiger shark. Cailliet et al. (1992) and Van Dykhuizen and Mollet (1992) also preferred the Gulland and Holt (1959) model over that of Fabens (1965) for the angel and sevengill sharks, respectively.

Data from this study indicated that neither tagging nor tagging combined with OTC injection appears to retard the growth rate in neonate and juvenile sharks up to 150 cm FL (Fig. 3). To the contrary, the growth rates from tagged sharks were higher than estimates obtained from vertebral growth bands (Table 3). The growth rates for the first two years of life for the tiger shark estimated from monthly length frequencies, tag-recapture (Gulland and Holt, 1959), and tag-recapture with OTC were all similar (Fig. 3). Tanaka (1990) found that growth rates of OTC-injected Japanese wobbegongs, *Orectolobus japonicus*, and neonate swell sharks, *Cephaloscyllium umbratile*, were not significantly different from controls. More recently, Gelsleichter et al. (1998) evaluated the toxicity of OTC on growth rates of captive nurse sharks, *Ginglymostoma cirratum*, and concluded that there were no adverse effects of OTC on growth rate. These data support the use of OTC as an effective method for determining vertebral band periodicity without interrupting normal growth patterns (Tanaka, 1990; Gelsleichter et al., 1998).

Our data do not verify nor refute age estimates for the tiger shark previously obtained from vertebral band counts (Branstetter et al., 1987) (Table 2; Fig. 2). The k value from our study is higher than Branstetter et al.'s (1987) Atlantic value and our L_∞ is lower. These differences are to be expected when comparing VBGF parameters from a conventional age-length (vertebral methods) study with those derived from a growth increment (tagging) study (Sainsbury, 1980; Francis, 1988). These types of curves are not directly comparable because the parameters are derived differently and, therefore, have different meanings (Francis, 1988). However, comparison of the estimates obtained in these studies to known values, such as size at birth and maximum size, can provide insight into the fit of the curves. This information allows us to determine which curve is best suited to be used for age at maturity and maximum age estimates. We believe that the current tag-recapture values are more accurate on the basis of verification available from the monthly length-frequency analysis and the consistency of the estimates to measurable parameters such as size at birth and maximum size. The L_∞ calculated by Branstetter et al. (1987) is lower than maximum reported sizes, and the size at birth (73 cm FL), based on the von Bertalanffy curve from that study, was high as related to known parameters (60–65 cm FL[1]).

Table 3

Size at age and growth per year for the tiger shark, *Galeocerdo cuvier*, calculated for tag and recapture data with Gulland and Holt's (1959) (this study) method compared with Branstetter et al.'s (1987) Atlantic vertebral data. Approximate size at maturity is indicated by bold typeface.

	Size (cm, FL)		
Age (years)	This study	Branstetter[1] 1987	This study growth/yr (cm)
Birth	61	73	
1	106	103	45
2	144	130	38
3	175	153	32
4	202	175	26
5	224	194	22
6	242	212	18
7	**258**	227	15
8	271	241	13
9	281	254	11
10	290	**265**	9
11	298	275	8
12	304	284	6
13	310	293	5
14	314	300	4
15	318	307	4
16	321	313	3
17	324	318	3
18	326	323	2
19	328	327	2
20	329	331	2

[1] Branstetter et al. (1987) values converted to FL

Statistically significant differences between age estimates from the Gulf of Mexico and North Atlantic populations of tiger shark found by Branstetter et al. (1987) may not be biologically significant (Yoccoz, 1991). The differences in age at maturity obtained between these two areas is only 2–3 years. Considering the relatively slow growth and large overlap of size at age for this species, a 2–3 year difference could be included in the realm of measurement error. In addition, we found statistically significant differences in growth by year in first year tiger sharks obtained from the same region over a period of five years. The differences in growth between years indicate that tiger shark growth is quite variable and probably dependent on fluctuations of many parameters in-

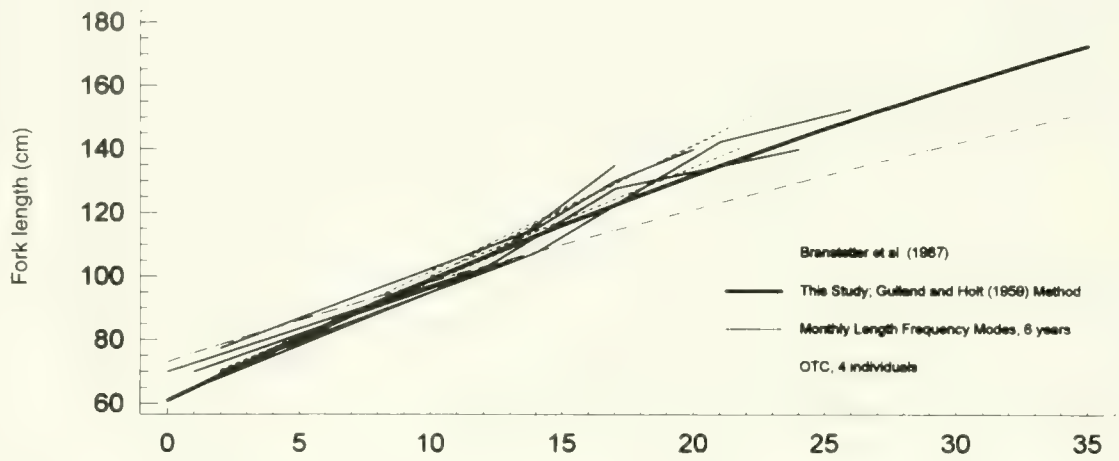

Figure 3

The von Bertalanffy growth curves from tag-recapture analysis was estimated with the Gulland and Holt (1959) model and the von Bertalanffy growth curve estimated from vertebral analysis (Branstetter et al. 1987). The solid lines represent the individual monthly length-frequency mode data from six year classes (1988–93). The initial points of the line are set by the size in June of the birth year. The solid lines are actual growth of four individual OTC-injected recaptured sharks at liberty over 0.9 yr. The length at tagging was used to obtain the initial age estimate to set the point on the graph.

cluding environmental conditions and prey availability. Our data show that that the majority of neonatal tiger sharks remain in the nursery area from birth until about 120–150 cm FL or 1.5–2 years of age.[1] It is known that tiger sharks frequently migrate into and out of the Gulf of Mexico (Kohler et al., in press). It is doubtful, with the migratory nature of this species and mixing between these areas, that growth rate differences in these groups are biologically significant past perhaps the first three years of life.

The longevity of the tiger shark is difficult to estimate. The NMFS tagging program has received data on five tiger sharks at liberty for 6 to 11 years. The oldest of these fish would have been 3+ years at tagging (185 cm FL, estimated), on the basis of the Gulland and Holt (1959) growth curve and, therefore, 14+ years at recapture (325 cm FL, measured). Branstetter et al.'s (1987) oldest aged tiger shark was 16 years of age. Our longevity estimate, based on a 7 half-life criterion, indicated that tiger sharks may live to be at least 27 years of age. Branstetter et al. (1987) estimated maximum age at anywhere from 20–37 years based on L_∞ for their various VBGF curves and rate of growth of large individuals.

Based on revised growth estimates presented in this study, estimated maximum age for this species is 27 years. Age at maturity, estimated from tag-recapture data from this study and size at maturity estimates from Branstetter et al. (1987), is seven years suggesting that females mature at 25% of their maximum age and may reproduce 10 times based on a two-year reproductive cycle.

Overall, the tiger shark is similar to other large carcharhinids in that it grows slowly and has a relatively long life, although it matures earlier than many other species in the northwest Atlantic (*C. leucas* 14–18 years, Branstetter and Stiles, 1987; *C. plumbeus* 15–30 years; Casey and Natanson, 1992, Sminkey and Musick, 1995; *C. obscurus* 19–20 years; Natanson, 1994; *C. falciformis* 6.5–12 years, Branstetter, 1987c, Bonfil et al., 1993). Branstetter (1987b) discussed the various life strategies of sharks on the basis of their k values. He suggested that tiger sharks, with k values from 0.11 to 0.16, fit into an intermediate category between slow growth species (k=0.05-0.10) such as *C. plumbeus, C. obscurus, Negaprion brevirostris,* and *Sphyrna lewini* and fast growth species ($k \geq 0.2$) such as *C. limbatus, C. brevipinna, Rhizoprionodon terraenovae*, and *Prionace glauca*. Other sharks in the intermediate group include *C. acronotus and C. falciformis* according to Branstetter (1987b). The tiger shark reaches maturity at a lower percent (25%) of its total age than do other carcharhinids for which this parameter has been estimated (*S. lewini* 33–50%, Branstetter, 1987c). This finding suggests that the tiger shark has a longer reproductive life span and possibly a greater reproductive potential than other carcharhinids.

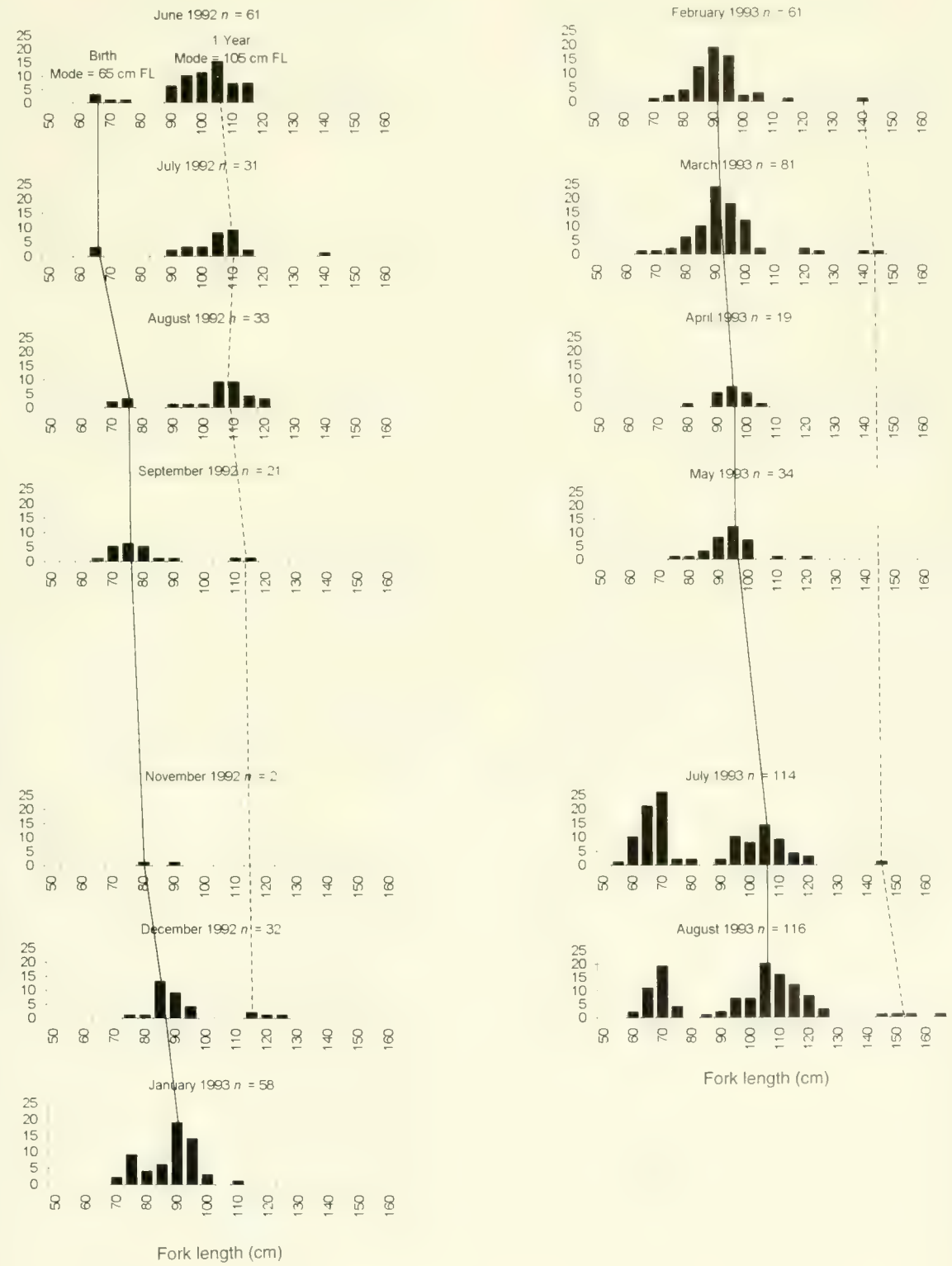

Figure 4

Monthly length-frequency data for the 1992 year class used for obtaining length-frequency growth rates for small (<160 cm FL) tiger sharks in the nursery area. First and partial second year growth for the 1992 year class is represented with the solid line. Second and partial third year growth for the 1991 year class is represented by the dashed line.

Casey and Natanson (1992) showed the advantage of using tag-recapture data over vertebral analysis for aging the sandbar shark. Cailliet et al. (1986) reviewed the techniques available for determining age and verifying age estimates in elasmobranchs. They pointed out that ages estimated from growth zones in calcified hard parts need to be verified with other methods, such as length-frequency and tag-recapture analyses. The authors also stressed the importance of validating the temporal periodicity of the calcified bands with tag-recapture data from the laboratory or field, coupled with OTC marking. Cailliet (1990), in an update of the Cailliet et al. (1986) review, listed the studies, to that date that had employed the various verification methods. Several of these used the combination of tag-recapture, length-frequency and OTC marking for verification or validation (or both) of the calcified structure age estimates. Growth estimates from a laboratory and field study of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Branstetter 1987a) corresponded well to estimates generated with length frequencies and vertebral rings (Parsons, 1985). Casey et al. (1985) used length-frequency, vertebral and tag-recapture analyses to verify age estimates for the sandbar shark, *C. plumbeus*, and concluded that there was close agreement with all three methods. Pratt and Casey (1983) also used these three methods to age the shortfin mako, *Isurus oxyrinchus*, and concluded that not only was there agreement between the methods but that tagging did not affect growth in this species. Smith (1984) validated the periodicity of vertebral band deposition in the leopard shark, *Triakis semifasciata* using OTC. Kusher et al. (1992) were able to confirm these results as well as use length-frequency data and additional tag-recapture data to produce independent age estimates for this species. The tag-recapture curve gave slower k values than the vertebral, and although the k values were not significantly different, the authors suggested that tagging may have had an effect on growth in this species (Kusher et al. 1992). These results accentuate the requirement of good tag and recapture data as a backup for vertebral studies, particularly if combined with OTC injections for validation. In the case of the tiger shark in this study, tag-recapture and length-frequency data have provided independent estimates of growth for verification. In addition, the results present evidence against the suggestion that tagging, with or without OTC injection, decreases the growth rate of sharks. It can be argued that the tiger shark cannot be used to generalize about sharks because they grow rapidly in relation to many other species. A birth size of 61 cm FL with a corresponding weight of 1.8 kgs. is small in relation to many large coastal species, such as the dusky shark (size and weight at birth: 81 cm FL and 7 kgs., respectively, Castro, 1983; Kohler et al., 1995) and the silky shark (size and weight at birth: 64 cm FL and 9 kgs., respectively). If these relatively small tiger shark young can withstand the rigors of tagging and continue to grow at a similar rate as untagged individuals, then it is certainly reasonable to believe that a larger shark can as well. Regardless, all species need to be evaluated individually for their reactions to tagging and OTC injection.

Acknowledgments

We are thankful to the thousands of fishermen who voluntarily tag and return tags to us and thus make this continuing program possible. We thank Chris Jensen who helped in tagging and injecting tiger sharks with tetracycline as well as providing accurate measurements on both tagged and recaptured specimens. Fisherman Eric Sander provided dozens of vertebrae from precisely measured recaptured young tiger sharks as well as from nontagged specimens. We also thank Steve Branstetter for discussions on the phone and for reviewing the manuscript. Greg Cailliet and Sabine Wintner also provided invaluable comments on the manuscript. We appreciate the encouragement and assistance of our colleagues in the Apex Predators Program.

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Recruitment of Atlantic croaker, *Micropogonias undulatus*: Do postsettlement processes disrupt or reinforce initial patterns of settlement?*

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Abstract.—Understanding the relative importance of pre- and postsettlement processes is critical to understanding the population dynamics of marine fishes. Our goals in this study were 1) to examine habitat preference and habitat use of newly settled Atlantic croaker, *Micropogonias undulatus*, and 2) to determine if postsettlement growth or predation varied with habitat type. Field surveys showed no difference in croaker abundance among three estuarine habitats: marsh edge, seagrass, and sand. Behavioral experiments in laboratory mesocosms suggested that the pattern of similar use of habitats in the field results from a lack of preference among habitats. In a field experiment, croaker recruitment was greater to artificial seagrass than to sand habitats, but there was no difference in fish density in habitats with or without food supplementation. Moreover, growth rates were similar in both sand and artificial seagrass habitats and in habitats with or without food supplementation. In a second experiment, we were unable to detect a difference in the density of newly settled croaker between sand and artificial seagrass habitats, or between habitats with predator access limited by cages and cage controls. Our results demonstrate that newly settled croaker use different estuarine habitats similarly, and there does not appear to be a fitness consequence of using many habitats. We suggest that for habitat generalists, such as the Atlantic croaker, variability in larval supply will be a stronger predictor of population dynamics than will variability of habitat attributes.

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Understanding the causes of fluctuations in population abundance is critical for ecologists and fishery biologists. For marine fishes with life histories in which adults have limited home ranges and larvae are pelagic and advected vast distances from natal sites, an understanding of variability in larval supply to local populations is critical for understanding the mechanisms that produce dynamics in populations (Caley et al., 1996). In addition, habitat selection by settling fish (Carr, 1991; Levin, 1991; Wellington, 1992; Tolimieri, 1995), and habitat-specific growth and mortality (Heck and Orth, 1980; Hixon and Beets, 1993; Levin et al., 1997) may ultimately reinforce or disrupt patterns created by variable larval supply (Jones, 1997). Thus, knowledge of the degree to which processes such as habitat selection, competition, or predation modify initial patterns of larval settlement is important in understanding the population dynamics of marine species.

The importance of variability in postsettlement growth or mortality and the level to which postsettlement processes alter initial patterns of larval settlement can be a function of habitat structure. For example, on coral reefs, holes provide a refuge from predation, and on reefs with large numbers of holes, the importance of predation is reduced (Shulman, 1984; Hixon and Beets, 1993). Similarly, Atlantic cod settle in equivalent densities in a variety of habitats but suffer lower predation rates in structurally complex habitats (Tupper and Boutilier, 1995). Thus, habitat-specific mortality disrupts initial patterns of larval settlement. Differences in habitat structure may also impact growth rates or the ability of fish to procure food (Nelson, 1979; Heck and Thoman, 1981; Stoner, 1982). As examples, 1) pinfish have greater success capturing amphipods in shoal grass (*Halodule wrightii*) than in similar densities of turtle grass (*Thalassia testudinum*) (Stoner,

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1982); 2) Atlantic cod grow faster in seagrass habitats than in sand, rocky reef, or cobble habitats (Tupper and Boutilier, 1995); and 3) pinfish exhibit higher growth rates in seagrass than in sand habitats (Levin et al., 1997).

Atlantic croaker, *Micropogonias undulatus* (hereafter referred to as croaker), range from Cape Cod to Campeche Bank, Mexico (Johnson, 1978), and occur both offshore and in estuaries in a variety of habitats including mud, sand, and seagrass (White and Chittenden, 1977; Johnson, 1978; Rooker et al., 1998). Croaker are an important component of commercial fisheries in the Gulf of Mexico and southeastern United States, often dominating bottom fish landings, and are an important sport fishery in this region (Lassuy, 1983). In the Gulf of Mexico, croaker spawn over the continental shelf or near inlets from September to May with peak levels occurring before January (Johnson, 1978; Cowan, 1988; Cowan and Shaw, 1988). Larval croaker then move toward shore and may be transported hundreds of kilometers before entering estuarine nursery grounds (Cowan and Shaw, 1988; Norcross, 1991). In Texas, recruitment of croaker peaks in November (Rooker et al., 1998). It is not clear whether variability in abundance of juvenile croaker is the result of variability in larval supply or differential postsettlement growth and mortality.

The delivery of larval croaker recruits to estuarine nursery habitats is dependent on large-scale oceanographic processes (Cowan and Shaw, 1988). Once fish arrive at estuaries, delivery into suitable habitats is dependent on currents and tidal processes (Norcross, 1991). As fish that are competent to settle approach nursery grounds they have the opportunity to choose specific microhabitats. In this paper we examined patterns of microhabitat preference and use by newly settled croaker, as well as the consequences of microhabitat associations. Specifically we asked 1) Do croaker have specific microhabitat preferences and are these preferences reflected in patterns of abundance in the field? 2) Does food supply limit the number or growth rates of croaker recruits in different habitats? 3) Does predation determine the number of recruits in different habitats?

Methods

Habitat use by newly recruited croaker

To determine what habitats newly recruited Atlantic croaker use, we conducted a field survey during November 1996 at Christmas Bay (29°03'N, 95°10'W), near Galveston, TX. Christmas Bay is a shallow estuary and contains the most easterly well-developed seagrass bed in Texas. A detailed description of this site can be found in Thomas et al. (1990). The seagrass bed is dominated by *Halodule wrightii* with an average density of 10,469 shoots/m^2 (SE=461). An epibenthic sled was used to quantify fish abundance in three habitats: bare sand, seagrass meadow, and marsh edge. We defined marsh edge habitat as the subtidal substrata directly adjacent to a *Spartina alterniflora* marsh. The sled consisted of a 0.66 m × 0.5 m opening fitted with a 3-m long net (1-mm mesh) with a removable codend. Habitats were sampled by placing the sled on the substratum, extending a 15-m rope in a semicircular fashion (to avoid disturbing sampling area) and pulling the sled through a 10-m^2 area. Each habitat was sampled four times at two different sites, resulting in eight samples per habitat type. Differences in croaker density were examined with a two-way analysis of variance with both site and habitat type as fixed effects. In this and subsequent analyses, if we failed to reject the null hypothesis of no difference in croaker abundance between habitats, then power analysis was performed. If statistical power was low, we calculated the number of replicates required to achieve sufficient power to accept the null hypothesis.

To examine habitat preference we performed choice experiments in laboratory mesocosms. Six 117-L mesocosms were constructed from round circular plastic tanks (41.3 cm diameter × 60 cm). The mesocosms were filled with 5 cm of sand, a plastic mesh screen was placed on top of the sand, and an additional 5 cm of sand was placed over the mesh. Each tank was filled with filtered seawater and maintained at ambient light and temperatures. We divided mesocosms in half, with each half randomly receiving a sand or grass habitat. Sand habitat was the sand bottom described above. To construct seagrass habitats, cores of seagrass were randomly collected from the field and brought to the laboratory where they were washed and dipped in fresh water. After leaves were wiped to remove any epiphytic growth, the cores were planted in each mesocosm.

One croaker (15–20 mm SL) was introduced to the center of each mesocosm and monitored for any abnormal behavior for 24 h. After the initial acclimation period, the location of each croaker was visually determined hourly for ten consecutive hours. Visual observations were performed by a single observer peering into the mesocosm, without disturbing the fish. This was repeated for six mesocosms over two days for a total of 12 mesocosm observations. New fish were used for each trial. Percent occurrence in each habitat was determined for all twelve trials. A one-way *t*-test determined if percent occurrence in seagrass was different from 50%.

Effects of food supply on recruitment and growth of croaker in varying habitats

Field experiments were conducted in East Lagoon, located at the eastern most end of Galveston Island, TX (29°20'N, 94°44'W). East Lagoon is 1.6 km long, 0.48 km wide, and has a maximum depth of 4.6 m. Water is exchanged tidally by means of seven 0.92 m-diameter cement culverts with the Galveston Ship Channel, which runs from the Gulf of Mexico into Galveston Bay. A detailed description of this site can be found in Levin et al. (1997). Seagrass, once widespread in Galveston Bay, including East Lagoon, has decreased by 90% from peak levels (Pulich and White, 1991); no natural seagrass habitats presently are found in East Lagoon. The absence of natural seagrass beds allowed us to establish artificial seagrass beds with desired characteristics, without the confounding effects of a natural seagrass bed. Experiments were located >8 m from the *Spartina alterniflora* dominated marsh edge and placed at an average low tide depth of 42 cm.

To test the null hypothesis that food supply does not limit abundance or growth rates of croaker recruits in different habitats, we conducted an experiment in which food supply was manipulated in sand and seagrass habitats. On 20 February 1996 we created five blocks each consisting of four 1-m^2 experimental plots. Within each block, food supply and habitat type were manipulated orthogonally. To control for differences in seagrass structure or seagrass-associated food resources, we used artificial seagrass habitats. Artificial seagrass habitats were constructed from a 1-m^2 polyvinylchoride (PVC) (1.3 cm diameter) frame, strung with monofilament to form a grid consisting of 576 points. At each of these points a 16 cm × .5 cm strand of green ribbon was woven in, such that the frame consisted of 576 shoots of seagrass, each shoot having two leaves. No excessive fouling was observed on the frame or ribbon for the duration of the experiment. We performed a preliminary experiment to determine if the structure of the PVC-frame would attract more fish recruits than bare sand, and no difference was found between the bare sand plot and the PVC-frame ($F_{2,23}$=0.512, α=0.61, 1–β=0.76). Consequently we performed subsequent experiments without a PVC-frame control.

Food supply was experimentally manipulated with feeding tubes in each experimental plot. Feeding tubes were constructed of a 7.5-cm diameter length of PVC pipe attached to a 1.3-cm diameter PVC pipe stake, with the bottom of the tube about 15 cm from the substratum, and the top always above the water line. We provided supplemental food daily for seven days, from 23 February to 3 March 1996, to half of the sand and seagrass replicates (i.e. five sand and five seagrass plots received food). Food consisted of 200 g of fish flesh and 300 mL of water blended to produce plankton-size particles (Forrester, 1990; Levin et al., 1997). The fish purée was placed in ice cube trays and frozen. Each frozen cube yielded 11.8 g of fish flesh. One cube of frozen food was placed in the feeding tubes of appropriate replicates, whereas control plots received one ice cube and no food was added. As the ice cube containing food melted, it delivered a continuous stream of particles to the habitat for 5–15 min. We observed fish readily consuming the supplemented food in both the field and laboratory.

On 4 March 1996, the experiment was terminated by sampling each plot. Recruit density was quantified by using 1 m^3 (1 × 1 × 1 m) drop samplers (Zimmerman et al., 1984; Fonseca et al., 1990). Drop samplers were constructed of 9.5-mm diameter rebar covered on four sides with taut 2-mm nylon mesh. A dip net (90 × 100 cm, 2-mm nylon mesh) was used to retrieve fish from the samplers, and replicates were considered adequately sampled when five consecutive passes of the dip net yielded no fish (Fonseca et al., 1990). A blocked two-factor analysis of variance was used to test the hypotheses that the abundance of newly recruited croaker did not vary among habitat or food supplemented treatments.

Five fish from each replicate were haphazardly selected for further analysis. We measured the 80 selected fish to the nearest 0.1 mm (SL), removed their otoliths, and stored them in immersion oil for one week. Fish age was then determined by enumerating the daily growth rings on the lapillar otolith by using an image analysis system. The existence of daily rings on croaker otoliths has been validated previously (Nixon and Jones, 1997). Each otolith was examined independently three times. If two of the three counts did not agree, the fish was discarded and another selected. When two of the three counts were the same, that count was used as a datum in the analysis.

Differences in growth rates were examined by using otolith microstructure. Because otolith diameter was correlated to fish length (r=0.73, n=75), we used otolith measures as a proxy for growth rate. Measurements were taken inward from the edge of the otolith to the seventh ring. This distance corresponded to growth during our seven days of food supplementation. Otolith distances (μ) were then converted into daily growth rates (mm SL/day), by using the following equation generated from a regression of otolith diameter on fish length:

$$Growth = [(otolith\ distance + 0.002) / 0.014]/7.$$

We used a blocked two-factor analysis of variance to test the hypothesis that growth rates did not vary among habitat or food supplementation treatments.

Effects of predation on recruitment of croaker to varying habitats

The null hypothesis that predation has no effect on recruitment of croaker in sand or seagrass habitats was tested by using cages to limit predator access to experimental plots. On 18 March 1996, a fortuitous seasonal low tide completely exposed the study site to air, allowing us to erect cages and to ensure that no recruits or predators occupied the cages at the start of the experiment. Cages ($2 \times 2 \times 1$ m) were constructed with 25-mm mesh on four sides, whereas cage controls had mesh on two sides. Mesh was large enough to be transparent to croaker recruits, but fine enough to prevent predators from entering the cages. A randomized block design was employed, with habitat (sand or grass) and predator access (cage or cage control) as fixed effects. Replicates were placed 8 m apart, and blocks were separated by 10 m. The experiment was terminated after 7 d. Drop samplers were used to quantify recruits as described previously.

Results

Habitat preference and use by newly recruited croaker

The density of newly settled croaker (mean TL=14.48, SE=0.15) did not differ among sand, seagrass, or marsh edge habitats ($F_{2,18}$=0.86, α=0.44, β=0.13) (Fig. 1). The density of croaker recruits also did not vary between sites ($F_{1,18}$=0.09, α=0.77) and the interaction between habitat and site was not significant ($F_{2,12}$=1.07, α=0.37).

Our observation on the behavior of croaker recruits in mesocosms did not reveal a preference between sand and seagrass habitats (one way t-test, t=1.64, df=11, α=0.13). An average of 36% (SE=16) of the time was spent in seagrass, and 64% (SE=16) in sand.

Effects of food supply on croaker recruitment and growth in varying habitats

The abundance of newly settled croaker differed between experimental habitats ($F_{1,11}$=5.98, α=0.03) with greater recruitment in sand ($\bar{X}$=31.6/m^2, SE=6.5) than in seagrass habitats ($\bar{X}$=13.7/m^2, SE=5.9) (Fig. 2). Conversely, we did not detect a difference ($F_{1,11}$=0.13, α=0.73) in the number of croaker in food-supplemented plots ($\bar{X}$=23.2/ m^2, SE=8.3), compared with control plots ($\bar{X}$=22.1/m^2, SE=4.1) (Fig. 2). The interaction between habitat and food-supplementation was not significant ($F_{1,11}$=0.96, α=0.35). The statistical power of this experiment was low (1–β=0.18);

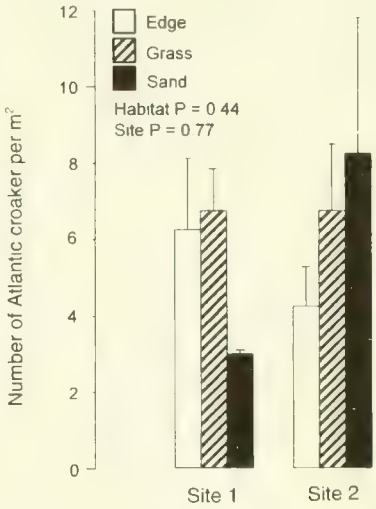

Figure 1

Atlantic croaker densities (mean +1 SE) sampled from three estuarine habitats: marsh edge (edge), seagrass bed (grass), and barren sand (sand). P values from two-way analysis of variance.

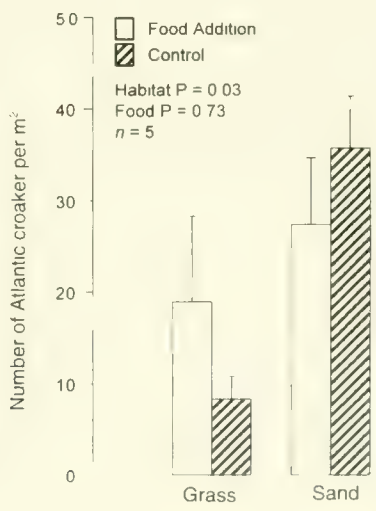

Figure 2

Atlantic croaker density (mean +1 SE) in 1-m^2 artificial seagrass (grass) and sand habitats, with (food addition) and without (control) food supplementation. P values from a blocked two-factor analysis of variance.

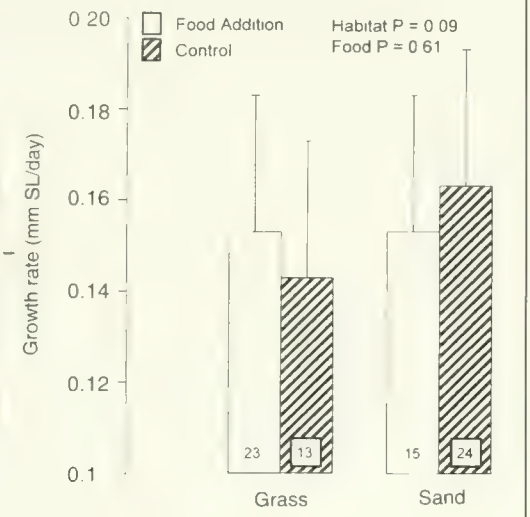

Figure 3

Growth rate (mean +1 SE) determined from analysis of otolith microstructure in croaker from 1-m^2 artificial seagrass (grass) and sand habitats with (food addition) and without (control) food supplementation. *P* values are from a blocked two-factor analysis of variance, and *n*, the number of fish sampled, is given at the base of each bar.

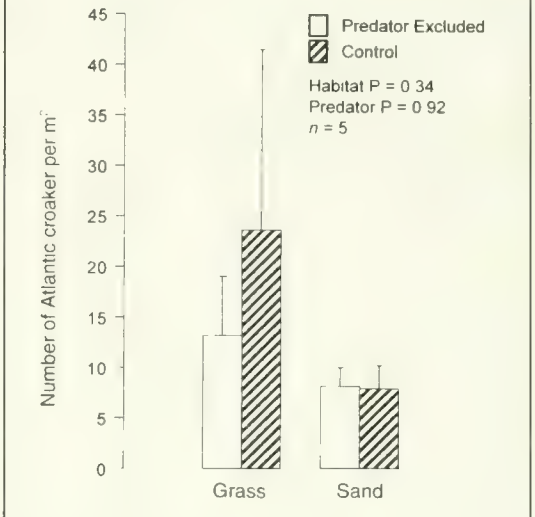

Figure 4

Atlantic croaker density (mean +1 SE) in 1 m^2 artificial seagrass (grass) and sand habitats with predators excluded and allowing predatory fish and decapod access (control). *P* values from a blocked two-factor analysis of variance.

however, given the small difference in average croaker density between food-supplementation and control plots (1.1/m^2) and the high within-treatment variation, we would have needed 55 replicates to achieve sufficient power ($1-\beta$=0.95) to accept the null hypothesis of no difference between treatment means.

Growth rates of newly recruited croaker were the same in sand and grass habitats ($F_{1,70}$=2.79, α=0.09, β<0.001), as well as with or without food supplementation ($F_{1,70}$=0.26, α=0.61, β=0.004) (Fig. 3). The interaction between habitat and food-supplementation on the growth rate of newly recruited croaker was not significant ($F_{1,70}$=0.49, α=0.49). Growth averaged 0.148 mm SL/day (SE=0.03) in grass and 0.158 mm (SE=0.03) in sand. Average growth rates of 0.153 mm/day (SE=0.03) were observed for both control and food addition treatments (Fig. 3). These growth rates are similar to growth rates reported elsewhere (Warlen, 1981; Cowan, 1988; Nixon and Jones, 1997), suggesting that our back calculation of growth rates from otolith measures were not seriously biased.

Effects of predation on recruitment of croaker to varying habitats

When we examined recruitment of croaker to experimental plots with or without predator access, we were unable to detect an effect of predation on croaker recruitment ($F_{1,12}$=0.01, α=0.92) (Fig. 4). Croaker density averaged 10.7/m^2 (SE=3.8) in the caged replicates, and 15.8/m^2 (SE=10.1) in cage controls (Fig. 4). In contrast with the food supplementation experiment, we did not detect a difference in recruitment between grass and sand habitats ($F_{1,12}$=0.96, α=0.34) (Fig. 4). The interaction between habitat and predator access was also not significant ($F_{1,12}$=0.10, α=0.76). This experiment also suffered from low power ($1-\beta$=0.06). Sufficient power to accept the null hypothesis of no difference in croaker density between cage and cage-control treatments ($1-\beta$=0.95), would have required 550 replicates.

Discussion

Recruitment of fishes with open populations is affected by variability in larval supply (Jenkins et al., 1996; Hamer and Jenkins, 1997), habitat selection by settling larvae (Bell et al., 1987) and postsettlement mortality (Orth et al., 1984), growth (Levin et al., 1997), and migration (Sogard, 1989). Understanding how these processes interact with each other to determine population size has been a major focus of researchers on tropical and temperate reefs (Doherty and Williams, 1988; Caley et al., 1996) and recently in seagrass meadows (Bell et al., 1987; Jenkins et al., 1996; Hamer and Jenkins, 1997). There has also

been a growing awareness that understanding how demographic processes vary with habitat structure will be critical for predicting population size in fishes that occur in heterogeneous habitats (Levin, 1994). In this study we examined patterns of abundance of newly settled Atlantic croaker and demonstrated that these fish use different estuarine habitats similarly. The results of our mesocosm experiment suggest that the pattern of similar recruitment in different habitats results from a lack of preference for specific habitats. In addition, when we investigated habitat differences in postsettlement growth or survivorship, we were unable to detect strong consequences of using one habitat over another.

We found no evidence suggesting that habitat selection by settling larvae and habitat-specific postsettlement mortality are important in determining population size in croaker; however, this conclusion is based on nonsignificant statistical tests rather than explicit acceptance of the null hypothesis of no difference between treatments. Recent reviews have stressed the importance of power analysis in detecting a type-II errors (Peterman, 1990; Reed and Blaustein, 1995; Thomas and Juanes, 1996), and because we wished to draw conclusions from "negative" results, power analysis was particularly important. In this study, when a difference between treatment means was not detected, we examined power in an attempt to determine our ability to accept the null hypothesis. If the power of the test was too low to accept the null hypothesis ($\beta \leq 0.05$), the number of replicates required to achieve this power level was calculated. For example, no difference was detected in mean croaker number between plots from which predators were excluded and control plots, but the power of this experiment was low ($1-\beta=0.06$). Sufficient power to be able to accept the null hypothesis, would have required 550 replicates. Our level of replication was inadequate because of the extreme variability in croaker densities among experimental plots—variation likely produced by a combination of stochastic settlement and habitat-specific mortality. The effect of this variability was to weaken the power of our experiments to detect small, but real differences among treatments. Although our experimental design precluded the detection of small treatment effects, the high number of replicates required to detect these small effects suggests that other processes are likely to be more important in determining variability in abundance.

Although many estuarine species select vegetated over unvegetated habitat at settlement (Orth et al., 1984), in some cases, initial patterns of settlement have little to do with habitat selection by individual organisms. Settlement may occur at the first suitable habitat encountered regardless of specific attributes of that habitat (Bell and Westoby, 1986). Additionally, current patterns may exclude delivery of competent larvae to some habitats (Morgan et al., 1996); therefore, even ideal habitats may seldom receive recruits. In such cases, larvae do not select against a habitat, instead that habitat is never an available choice. By experimentally providing habitats, and by using a blocked sampling design such that all habitats were available in a particular location, we eliminated the possibility that settling croaker would not have the opportunity to choose a habitat. In our field sampling and experiments, croaker had the opportunity to choose between vegetated and unvegetated habitats, but they did not consistently choose one habitat over another. By contrast, in an identical experiment performed at the same time and in the same study site, pinfish (*Lagodon rhomboides*) showed strong responses to habitat, food supply, and predators (Levin et al., 1997). Pinfish occurred in much higher densities in vegetated than in unvegetated habitats and also grew faster in grass habitats supplemented with food than in unsupplemented or unvegetated habitats. In addition, the presence of predators reduced pinfish numbers by 50%. The pinfish and croaker occupying experimental plots were similar in size (15–25 mm SL), and at this size the diets of the two species are similar (Darcy, 1985; Soto et al., 1998). Thus, it is likely that the lack of response by croaker to the habitat attributes we investigated is the result of characteristics of the species rather than an artifact of sampling or experimental design.

Selection for specific habitats at settlement may overwhelm variation in larval supply, thus producing variability in recruitment that is associated with the preferred habitat. This appears to be the case for pinfish (Levin et al., 1997). Although croaker often form part of fish assemblages within seagrass (Rooker et al., 1998), they appear to have broad microhabitat preferences, and our results suggest that there is no strong fitness consequences for croaker using vegetated versus unvegetated habitats. As a result, resources associated with the benthic habitat seem unlikely to determine population size of newly recruiting croaker. Rather, where and when larvae that are competent to settle are delivered should determine population size in croaker. The contrasting results for croaker and pinfish may reflect a more general difference in the processes determining population sizes of fish. For fishes, such as pinfish, where settling larvae select specific habitats and postsettlement processes reinforce initial settlement patterns, spatial and temporal variability in habitat should be a strong predictor of future

population size. Habitat generalists, such as croaker, can occupy a range of habitats in any particular location, and thus variability in a specific resource may not determine population size. Consequently, processes affecting larval supply will be more important predictors of population size than resource-related characteristics.

Generalizations about the relative importance of processes affecting recruitment in fishes have been elusive (Caley et al., 1996). Although it is widely recognized that understanding the roles of both pre- and postsettlement is critical, there is still little consensus on the relative importance of different processes in determining population size. We suggest that neglecting the behavioral and ecological characteristics of individual species may be a major obstacle in reaching widely accepted generalizations about processes affecting recruitment. By performing similar experiments on different species we may uncover generalizations about processes affecting fish populations that have thus far been difficult to attain.

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Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska

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Abstract.—Nearshore and shelf fish communities were studied in three areas of lower Cook Inlet, Alaska: the Barren Islands (oceanic and well-mixed waters), Kachemak Bay (mixed oceanic waters with significant freshwater runoff), and Chisik Island (estuarine waters). Fish were sampled with beach seines (n=413 sets) and midwater trawls (n=39 sets). We found that lower Cook Inlet supported a diverse nearshore fish community of at least 52 species. Fifty of these species were caught in Kachemak Bay, 24 at Chisik Island, and 12 at the Barren Islands. Pacific sand lance dominated Barren Islands and Kachemak Bay nearshore habitats, comprising 99% and 71% of total individuals, respectively. The nearshore Chisik Island fish community was not dominated by any one species; instead it exhibited higher diversity. These spatial differences appeared linked to local oceanographic regimes and sediment influx. Analysis of historical data revealed that the nearshore Kachemak Bay fish community changed significantly between 1976 and 1996, showing increased diversity and abundance in several taxa, notably gadids, salmonids, pleuronectids, and sculpins. Decadal differences appeared to be related to large-scale climate changes in the North Pacific. Catches of most taxa peaked in May–August, and were low during other months of the year. Several species were present for only part of the summer. Species composition of seine catches differed significantly between consecutive high and low tides, but not between consecutive sets or years. Midwater trawls took 26 species, 14 of which were present in Kachemak Bay, 19 near Chisik Island, and 7 at the Barren Islands. Community structures in shelf and nearshore waters were similar: diversity was high and abundance low at Chisik Island, whereas a few abundant species dominated at both Kachemak Bay and the Barren Islands. In addition, the low fish abundance near Chisik Island appeared to be related to declining seabird numbers at this colony.

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Dramatic changes in seabird and marine mammal populations in the Gulf of Alaska have been linked to shifts in abundance and composition of forage fish stocks over the past 20 years (Piatt and Anderson, 1996; Anderson et al.[1]). Coincident with cyclical fluctuations in seawater temperatures, abundance of several key forage species, including capelin (*Mallotus villosus*), pricklebacks (mostly *Lumpenella longirostris*), and Pacific sandfish (*Trichodon trichodon*) declined precipitously in the late 1970s. Meanwhile populations of large predatory fish, including walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and several pleuronectids increased dramatically. Correspondingly, seabird diets shifted from mostly capelin in the 1970s to mostly Pacific sand lance (*Ammodytes hexapterus*) and juvenile pollock by the late 1980s (Piatt and Anderson, 1996). Furthermore, a variety of seabirds and marine mammals exhibited signs of food stress during the 1980s and early 1990s (Piatt and Anderson, 1996). Inferences about changes in Gulf of Alaska fish communities have been based on a limited number of site-specific long-term studies (e.g. Anderson et al.[1]); however, evidence is mounting that suggests these changes were wide-spread throughout the region (Francis et al., 1998).

The importance of inshore marine habitats as nursery areas for juveniles of many marine fish species has been well reported (Poxton et al., 1983; Orsi and Landingham, 1985; Bennett, 1989; Blaber et al., 1995; Dalley and Anderson, 1997). Studies in other parts of the world

[1] Anderson, P. J., S.A. Payne, and B. A. Johnson. 1994. Multi-species dynamics and changes in community structure in Pavlof Bay, Alaska 1972–1992. Natl. Mar. Fish. Serv., NOAA, Kodiak, Alaska. Unpubl. manuscript, 26 p.

have also described seasonal variation in shallow water fish assemblages (e.g. Horn, 1980; Allen, 1982; Nash and Gibson, 1982; Nash, 1988; Bennett, 1989). Little is known, however, about annual, seasonal, and daily variation in fish abundance in Alaska. Understanding the responses of fish populations at this scale are critical for examining finer-scale processes such as trophic interactions. Responses at these time scales also put interdecadal changes into perspective, and it is changes at the decadal scale that are rapidly becoming the focus of fishery oceanographers (Francis et al., 1998).

Our primary objectives were to assess variability in abundance, diversity, and distribution of nearshore fishes in three oceanographically distinct locations within lower Cook Inlet and to compare these data with information collected by Blackburn et al. (1980) 20 years ago. Until our study, Blackburn et al.'s 1976 surveys provided the only comprehensive description of nearshore fish communities in the region. Concurrent sampling of offshore species with midwater trawls also allowed us to make comparisons between shelf and nearshore fish communities.

Methods

Study sites

Lower Cook Inlet (Fig. 1), in south-central Alaska, is the largest embayment in the northern Gulf of Alaska. The area supports several important seabird colonies and numerous marine mammals, as well as important commercial and recreational fisheries for salmon (*Oncorhynchus* spp.) and Pacific halibut (*Hippoglossus stenolepis*). We studied three lower Cook Inlet areas that primarily support colonies of fish-eating common murres (*Uria aalge*) and black-legged kittiwakes (*Rissa tridactyla*): Gull Island, in Kachemak Bay; Chisik Island, on the western side of Cook Inlet; and the Barren Islands, near the entrance to Cook Inlet. Investigations of nearshore fish communities were initiated around these colonies to provide information that can be used to improve understanding of how forage fish abundance and distribution may influence seabird diets and productivity in these areas.

Kachemak Bay (Fig. 1) lies along the southeastern shore of Cook Inlet. The bay is 38 km wide at its entrance and 62 km long. The upper 6 km consists of mud flats that are exposed during low tide. Depths are relatively shallow, ranging from about 35 to 90 m, with some deeper areas (100 to 165 m) present off Gull Island along the south-central side of the bay. Water entering the bay originates from the Gulf of Alaska and is largely oceanic (Fig. 1; Burbank, 1977).

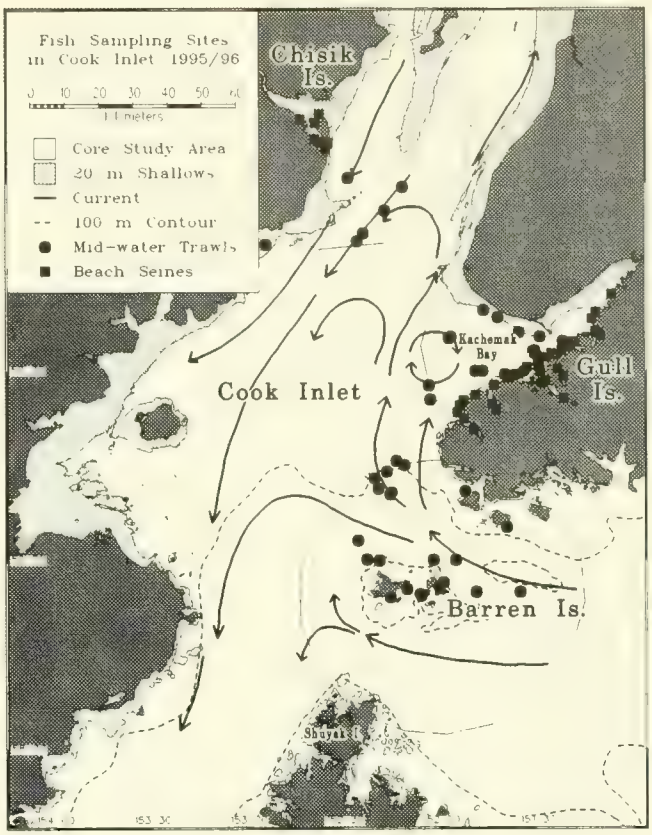

Figure 1

Map of lower Cook Inlet showing the three study areas, prevailing currents, bathymetry, and both beach seine and midwater trawl locations.

Chisik Island, on the western side of Cook Inlet (Fig. 1), is located in the mouth of Tuxedni Bay, which receives freshwater from glacier-fed rivers. Water passing outside the island is also estuarine, because it receives significant glacier-fed freshwater input from large rivers at the head of Cook Inlet before circulating down the western side of the inlet (Burbank, 1977; Feely and Massoth, 1982). Nearshore habitats around Chisik Island contain few sandy substrates and consist primarily of glacial silt and mud flats interspersed with rocky substrates that are exposed at low tides.

The Barren Islands, near the entrance to Cook Inlet (Fig. 1), are situated in a transition zone between deep Gulf of Alaska waters and the shallow Cook Inlet estuary. The Alaska Coastal Current enters Cook Inlet north of the Barren Islands, leading to intense upwelling of cold, nutrient-rich waters onto the shallow southeastern Cook Inlet shelf (Burbank, 1977). Because of the upwelling and strong tidal action (second highest tidal range in North America), waters in this area are turbulent and well mixed.

Field collections

We used beach seines to sample nearshore fish communities. These nets effectively and nonselectively sample shallow, inshore waters with sandy or smooth bottoms (Cailliet et al., 1986). In Kachemak Bay, samples were obtained during 16 June–26 July 1995 and 8 February–10 December 1996. Weather and sea conditions prevented sampling in January and November 1996. Sampling at Chisik Island and the Barren Islands occurred during 3 July–17 August, and 26 June–8 September 1996, respectively.

Our variable-mesh nets were 44 m long. The middle 15.3-m-long, 4-m-deep section was made of 3-mm knotless nylon stretch mesh (sm), and the wings tapered to a depth of 2.3 m were constructed of 13-mm knotted sm nylon. Thirty meters of rope were attached to the ends for deployment. Blackburn et al. (1980) used similar-size seines to sample Kachemak Bay in 1976. Nets were set parallel to shore about 25 m from the beach as described by Cailliet et al. (1986). Samples were collected about every two weeks in Kachemak Bay during May–September, and once a month throughout the winter. Samples from Chisik Island and the Barren Islands were collected every two weeks for the duration of their field seasons.

We sampled 38 Kachemak Bay sites that were seined by Blackburn et al. (1980) in 1976. At these sites, we made 60 and 245 sets during May–September of 1995 and 1996, respectively. In comparison, Blackburn et al. made 131 sets during May–September 1976. Raw data from the 1976 study were obtained from J. Blackburn, Alaska Department of Fish and Game (ADF&G), Kodiak, Alaska.

Sets were made at eight sites on the west side of Chisik Island. Twenty-three of these sets were made at high tide and seven at low tide (low tide sets were limited by deep mud in the subtidal zone). At the Barren Islands, 40 sets (18 at high tide and 22 at low tide) were made in Amatuli Cove.

Beach seining was conducted within one-hour windows on either side of high and low tides. To assess tidal influence on catch rates, seven sites in Kachemak Bay were seined regularly on consecutive high and low tides during periods of maximum tidal oscillation (about every 15 days). A single set usually provides good representation of species richness and dominant species rank (Allen et al., 1992). However, to assess variability of beach seine catches, two consecutive sets were made adjacent to each other at the seven sites intensively studied at each tidal stage. As a result, these sites were sampled four times on each day that seining occurred. Fish were sorted and counted by species. Owing to the key trophic role of sand lance in the Gulf of Alaska (Blackburn and Anderson, 1997), these fish were also separated into adult (age groups ≥1) and juvenile (age group 0) categories on the basis of otolith interpretations.

Midwater trawls were used to sample offshore shelf environments by using the ADF&G 22-m stern trawler RV *Pandalus* in July 1996. Forage fish were located with a Biosonics DT4000 digital echosounder (120 kHz), and significant targets were fished by using a modified herring trawl with a 50-m^2 opening. Mesh sizes diminished stepwise from about 5 cm in the wings to 1 cm at the codend. The codend was lined with 3-mm mesh and contained a collecting bucket. Trawls were monitored with a Furuno net-sounding system. Tow duration ranged from 20 to 60 minutes depending on fish concentrations. Midwater trawls were not directly comparable to beach seines; trawls selectively sampled the pelagic zone, whereas beach seines unselectively sampled both pelagic and demersal zones.

Analyses

We calculated four indices to assess broad differences between sites and sampling periods. The Shannon-Wiener index (H') indicates diversity; it increases as both the species number (richness) and equitability of species abundance (evenness) increase (Pielou, 1977). To measure species "richness" in diversity, we used Margalef's index (D; Margalef, 1968), and to assess equitability of species abundance, we calculated Pielou's evenness function (J'; Pielou, 1977). Similarity between species lists from different sampling periods was tested by using Jaccard's similarity coefficient for presence and absence data (Boesch, 1977). All diversity calculations were based on numbers of individuals and were made with natural logs ($\log_e$). Species assemblages were compared statistically with the Mann-Whitney rank sum test.

Results

Interdecadal comparison of beach seine catches in Kachemak Bay: 1976 versus 1995–96

Beach seines were an efficient method of catching nearshore fish. Of the 305 sets made in Kachemak Bay during May–September in 1995 and 1996, only four failed to yield fish. A total of 155,991 fish comprising 50 species were caught in these seines (Table 1). Of these species, 35 were primarily represented by juvenile stages. All species found during winter were also present during summer. Sand lance were most numerous; they represented 71% of total individuals.

Table 1

Frequency of occurrence and catch-per-unit-of-effort (CPUE) by species caught in beach seines during 1976 (May 21–September 29) and 1995/96 (May 16–September 27).

			1976[1] (131 Sets)		1995–96 (305 Sets)			
Status	Common name	Scientific name	% Occurence	CPUE	% Occurrence	CPUE	Change in % Occurrence[2]	Change in CPUE[3]
Abundant								
>50% of sets in at least one of the time periods	Dolly varden	*Salvelinus malma*	51.1	6.03	46.6	5.36	=	=
	Pacific sand lance	*Ammodytes hexapterus*	40.5	248.02	50.8	363.28	=	=
	Great sculpin	*Myoxocephalus polyacanthocephalus*	32.8	0.92	56.7	1.59	=	=
Common								
10–50% of sets in at least one of the time periods	Pink salmon	*Oncorhynchus gorbuscha*	24.4	6.14	39.0	28.16	=	=
	Rock sole	*Pleuronectes bilineatus*	15.3	0.33	30.2	1.24	=	=
	Pacific herring	*Clupea pallasi*	14.5	35.62	17.4	64.94	=	=
	Pacific cod	*Gadus macrocephalus*	0.8	0.01	27.2	14.49	+++	+++
	Whitespotted greenling	*Hexagrammos stelleri*	10.7	0.25	17.0	0.68	=	=
	Tubenose poacher	*Pallasina barbata*	5.3	0.07	15.7	0.42	+	=
	Threespine stickleback	*Gasterosteus aculeatus*	13.0	0.27	6.2	0.14	--	=
	Chinook salmon	*Oncorhynchus tshawytscha*	12.2	2.20	5.6	0.25	--	=
	Surf smelt	*Hypomesus pretiosus*	11.5	1.36	4.9	0.16	–	=
	Silverspotted sculpin	*Blepsias cirrhosus*	0.8	0.01	13.8	0.51	+++	+
Occasional	Snake prickleback	*Lumpenus sagitta*	6.9	0.41	5.6	0.58	=	=
1–10% of sets in at least one of the time periods	Chum salmon	*Oncorhynchus keta*	3.1	0.06	7.5	2.58	++	++
	Saffron cod	*Eleginus gracilis*	1.5	0.02	8.9	1.71	+++	+
	Pacific staghorn sculpin	*Leptocottus armatus*	6.1	0.09	3.3	0.04	=	=
	Sockeye salmon	*Oncorhynchus nerka*	0.8	0.01	8.5	2.54	+++	++
	Pacific tomcod	*Microgadus proximus*	0.0	<0.01	9.2	2.16	+++	+++
	Crescent gunnel	*Pholis laeta*	2.3	0.04	4.9	0.19	+	=
	Starry flounder	*Platichthys stellatus*	3.8	0.05	2.6	0.15	=	=
	Pacific sandfish	*Trichodon trichodon*	0.0	<0.01	6.2	0.15	+++	+++
	Kelp greenling	*Hexagrammos decagrammus*	0.0	<0.01	4.6	0.15	?[4]	?[4]
	Buffalo sculpin	*Enophrys bison*	0.8	0.02	3.6	0.08	+++	=
	Slender eelblenny	*Lumpenus fabricii*	0.0	<0.01	4.3	0.88	+++	+++
	Masked greenling	*Hexagrammos octogrammus*	3.8	0.15	0.3	0.01	---	--
	Rock greenling	*Hexagrammos lagocephalus*	0.0	<0.01	3.6	0.15	?[4]	?[4]
	Lobefin snailfish	*Liparis greeni*	0.0	<0.01	3.3	<0.01	+++	+++
	Lingcod	*Ophiodon elongatus*	1.5	0.02	1.3	0.02	=	=
	Butter sole	*Pleuronectes isolepis*	1.5	0.02	1.3	0.01	=	=
	Walleye pollock	*Theragra chalcogramma*	0.0	0.00	2.6	4.62	+++	+++
	Coho salmon	*Oncorhynchus kisutch*	1.5	0.50	0.7	0.01	--	--
	Warty sculpin	*Myoxocephalus verrucosus*	0.0	0.00	2.0	0.04	+++	+++
	Sablefish	*Anoplopoma fimbria*	0.0	0.00	1.6	0.17	+++	+++
	Longsnout prickleback	*Lumpenella longirostris*	1.5	0.06	0.0	0.00	---	---
	Daubed shanny	*Lumpenus maculatus*	0.0	<0.01	1.3	0.02	+++	+++

continued

Pacific herring (*Clupea pallasi*), pink salmon (*Oncorhynchus gorbuscha*), walleye pollock, and Pacific cod accounted for 22% of the remaining individuals. Great sculpin (*Myoxocephalus polyacanthocephalus*), sand lance, and Dolly Varden (*Salvelinus malma*) were the most frequently caught species during 1995–1996, each occurring in over 40% of the samples.

Table 1 (continued)

Status	Common name	Scientific name	1976[1] (131 Sets) % Occurence	1976[1] (131 Sets) CPUE	1995/96 (305 Sets) % Occurrence	1995/96 (305 Sets) CPUE	Change in % Occurrence[2]	Change in CPUE[3]
Rare								
<1% of sets in	Flathead sole	*Hippoglossoides elassodon*	0.0	<0.01	1.3	0.02	+++	+++
both time periods	Northern rockfish	*Sebastes polyspinis*	0.8	<0.01	0.7	0.01	[5]	-
	Sawback poacher	*Sarritor frenatus*	0.8	<0.01	0.3	<0.01	[5]	[5]
	Soft sculpin	*Psychrolutes sigalutes*	0.0	<0.01	1.0	0.02	[5]	[5]
	Petrale sole	*Eopsetta jordani*	0.0	<0.01	1.0	0.04	[5]	[5]
	Prowfish	*Zaprora silenus*	0.0	<0.01	0.7	0.01	[5]	-
	Padded sculpin	*Artedius fenestralis*	0.0	<0.01	0.7	0.01	[5]	-
	Pacific halibut	*Hippoglossus stenolepis*	0.0	<0.01	0.7	0.01	[5]	
	English sole	*Pleuronectes vetulus*	0.0	<0.01	0.7	0.01	[5]	[5]
	Capelin	*Mallotus villosus*	0.0	<0.01	0.3	<0.01	-	[5]
	Arctic shanny	*Stichaeus punctatus*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Yellow Irish lord	*Hemilepidotus jordani*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Ribbed sculpin	*Triglops pingeli*	0.0	<0.01	0.3	<0.01	-	
	Smooth alligatorfish	*Anoplagonus inermis*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Smooth lumpsucker	*Aptocyclus ventricosus*	0.0	<0.01	0.3	<0.01	-	[5]

[1] 1976 data also includes: 28% sets with unidentified sculpins and 25% sets with unidentified greenlings. Data from J. Blackburn (Alaska Dept Fish and Game, Kodiak).

[2] Change in frequency of occurrence between 1976 and 1995–96 defined by = (<100% change in frequency), + or – (100–200% change), ++ or -- (200–300% change), or +++ or --- (>300 % change).

[3] Change in CPUE between 1976 and 1995/96 defined by = (values within an order of magnitude), + or – (values changed by one order of magnitude), ++ or -- (values changed by two orders of magnitude), and +++ or --- (values changed by at least three orders of magnitude).

[4] Unidentified greenlings in 1976 were a mix of rock and kelp greenlings.

[5] CPUE and frequency of occurrence were too small to infer change.

In 1976, a total of 39,927 fish comprising at least 28 species were collected from 131 seine sets (greenling, Hexagrammidae, and sculpins, Cottidae, were not always identified to species; Blackburn et al., 1980; Table 1). To compare these data statistically with 1995–96 information, sculpin and greenling were combined into two general categories. By number, sand lance (81%) and herring (12%) accounted for more than 93 % of the 1976 catch. Four of the five species that dominated 1976 catches also dominated the 1995–96 catches (sand lance, herring, Dolly Varden, and pink salmon), and sand lance and herring were the two most abundant fish caught during both study periods. In 1976, only four (0.01%) fish were gadids (3 saffron cod, *Eleginus gracilis*; and 1 Pacific cod). By 1995–96, gadids (Pacific cod; saffron cod; Pacific tomcod, *Microgadus proximus*; and walleye pollock) were more numerous on the basis of catch-per-unit-of-effort (CPUE, defined as catch-per-individual-seine) by 1–3 orders of magnitude and had increased in frequency of occurrence by more than 300% (Table 1). Furthermore, Pacific cod was a dominant species in the 1995–96 catches. Similar increases in CPUE or frequency of occurrence were apparent for sockeye and chum salmon (*O. nerka*, *O. keta*), three sculpin species (silverspotted sculpin, *Blepsias cirrhosus*; buffalo sculpin, *Enophrys bison*; warty sculpin, *Myoxocephalus verrucosus*), Pacific sandfish, two prickleback species (slender eelblenny, *Lumpenus fabricii*; daubed shanny, *L. maculatus*), lobefin snailfish (*Liparis greeni*), sablefish (*Anoplopoma fimbria*), and a flatfish species (*Hippoglossoides elassodon*). Marked declines only occurred in catches of masked greenling (*Hexagrammos octogrammus*), coho salmon (*O. kisutch*), and longsnout prickleback (*Lumpenella longirostris*). Differences between 1976 and 1995–96 catches were significant on the basis of change in CPUE (Mann-Whitney rank sum test; t=1339.5, P=0.007), percent composition (t=1373.0, P=0.018), and frequency of capture (t=1398.0, P=0.033).

Changes in fish abundance were accompanied by changes in community diversity (Table 2). The Shannon-Wiener index (H') was greater in 1995–96 than in 1976, reflecting the large increase in gadid species during the 1990s (accounting for two thirds of the difference in H'). Species richness (D) was also higher in 1995–96, compared with 1976. This difference resulted from the fact that four species represented 92% of the total 1995–96 catch. In contrast, only two species accounted for 93% of the 1976 catch.

Table 2

Catch-per-unit-of-effort (CPUE) and species diversity indices from nearshore and shelf areas of Kachemak Bay (1976 and 1995–96), Chisik Island, and the Barren Islands. Diversity indices: H' = species diversity; J' = species evenness function; D = species richness (see "Methods" section).

		CPUE		H'		J'		D	
Location	Year	Nearshore	Shelf	Nearshore	Shelf	Nearshore	Shelf	Nearshore	Shelf
Kachemak Bay	1976	305	—	0.74	—	0.23	—	2.27	—
Kachemak Bay	1995–96	511	345	1.05	1.07	0.29	0.40	3.26	1.51
Chisik Island	1996	33	92	2.13	1.89	0.67	0.64	3.34	2.85
Barren Islands	1996	4506	821	0.06	0.31	0.03	0.16	0.91	0.63

Table 3

Comparison of 1995 and 1996 Kachemak Bay beach seine catches for species that occurred in more than 10% of sets.

	1995			1996		
Species	Frequency of capture	Percent of total catch	CPUE	Frequency of capture	Percent of total catch	CPUE
Pacific sand lance	75.0	66.6	310.2	67.2	60.0	250.1
Dolly varden	68.3	1.8	8.5	55.7	1.8	7.5
Great sculpin	68.3	0.7	3.2	49.2	0.2	1.0
Pink salmon	51.7	3.0	14.0	52.5	13.8	57.4
Rock sole	33.3	0.2	1.0	36.9	0.4	1.5
Pacific cod	41.7	7.4	34.4	18.9	0.5	2.2
Pacific herring	30.0	16.1	75.1	11.5	16.5	68.8
Whitespotted greenling	20.0	0.2	0.9	21.3	0.1	0.5
Tubenose poacher	31.7	0.3	1.3	11.5	>0.1	0.2
Silverspotted sculpin	20.0	0.2	0.8	17.2	0.1	0.5

The low equitability (J') in both time periods reflected dominance by a few species (e.g. sand lance, herring) in catches.

Jaccard's similarity coefficient indicated only moderate (59%) similarity in the presence-absence of species between 1995–96 and 1976. This may have resulted from a combination of 1) a dramatic increase in abundance of some species in 1995–96 (e.g. tomcod, sandfish); and 2) increased fishing effort in 1995–96, which may have increased catches of less common species (e.g. prowfish, *Zaprora silenus*; capelin) that might have also been detected in 1976, if fishing effort had been greater.

Interannual comparison of beach seine catches in Kachemak Bay: 1995 versus 1996

As evidenced by catches of common species in Kachemak Bay (Table 3), there was little obvious difference in catches between consecutive years. During June and July of 1995, 27,944 fish belonging to 42 species were caught in 60 beach seine sets (CPUE=466). During the same period in 1996, 50,859 fish representing 37 species were found in 122 sets (CPUE=417). Forty-four species were identified over the course of the two year study, of which 30 were caught in both years. Species diversity (H') was similar in 1995 and 1996 (1.21 and 1.22, respectively), as were species richness (D; 3.61 and 3.43, respectively) and equitability (J'; 0.34 in both years).

Jaccard's similarity coefficient indicated a 68% similarity between the species assemblages caught in 1995 and 1996. Species not represented in one year or the other were generally uncommon species that were found in only a few seine sets. Differences in percent composition of 1995 and 1996 species assemblages were not significant (Mann-Whitney rank sum test).

Seasonal variation in the nearshore fish community of Kachemak Bay

To examine seasonal variation in nearshore fish abundance, we used only data collected in 1996 (130,325 fish, 46 species, 283 beach seine sets in February–December). Most species were present in greatest numbers during summer months, apparently moving inshore as water temperatures increased above 4°C in May (Fig. 2), and moving offshore as temperatures declined in October (Fig. 3). Almost no fish were caught or observed during the winter months (December–March; Fig. 3); however, CPUE increased markedly for all species in June and declined dramatically in mid-July. This pattern was also reported by Blackburn et al. (1980; Fig. 4). This change largely resulted from changes in nearshore sand lance abundance but was compounded by movements of pink salmon and Pacific cod. Large catches of juvenile pink salmon increased the CPUE in June as they migrated along shorelines (Orsi and Landingham, 1985), but salmon CPUE declined rapidly in July as fish moved offshore (Fig. 3; Blackburn et al., 1980). Catches of gadids (particularly Pacific cod and pollock) increased markedly in late summer (Fig. 3) and contributed to the large August increase in CPUE. However, most of the August–September increase in CPUE was due to recruitment of first-year sand lance (Fig. 3), which dominated late summer seine catches after adults moved out of nearshore environments in late July (Blackburn et al., 1980). In October, adult sand lance returned to inshore waters to spawn (Dick and Warner, 1982; Robards, 1999). CPUE began declining rapidly in October, in conjunction with a decline in diversity from 34 species in August to only 3 by December.

We also observed strong seasonal trends in use of nearshore habitats by other species. Dolly Varden moved into nearshore waters in April, where they remained throughout July. After July they followed salmon into natal freshwater systems to overwinter (Isakson et al., 1971, Orsi and Landingham, 1985). Juvenile rock sole (*Pleuronectes bilineatus*) and great sculpins were consistently the most abundant fish found in nearshore habitats during February–March. Flatfish (Pleuronectidae) were caught at low rates throughout spring and summer but were not present after October (Fig. 3). Numbers of juvenile great sculpins increased rapidly in spring owing to an influx of small juveniles (<20 mm). Catches of these juveniles fell markedly by late June, and small but regular numbers of second-year individuals were caught during summer. Only one capelin was caught in Kachemak Bay (26 July 1995) prior to October 1996, when 1586 first-year fish were captured in three seine sets. Several large capelin schools were also observed at the same time. Capelin were also captured in three of eight seine sets in December. Although herring were present throughout the summer (Fig. 3), almost all of them (99%) were captured in five June and four August sets at one area (Halibut Cove) historically known for its aggregations of herring (Rounsefell, 1930).

Species abundance, diversity (H'), and richness (D) in the nearshore Kachemak Bay fish community increased steadily from April to June, peaked in July, and declined rapidly in September. Although sand lance dominated the community in summer, more than 30 species of fish were present during June–August. Species evenness (J') declined throughout summer, when sand lance dominated nearshore habitats, but increased again in fall as numbers of species and individuals declined.

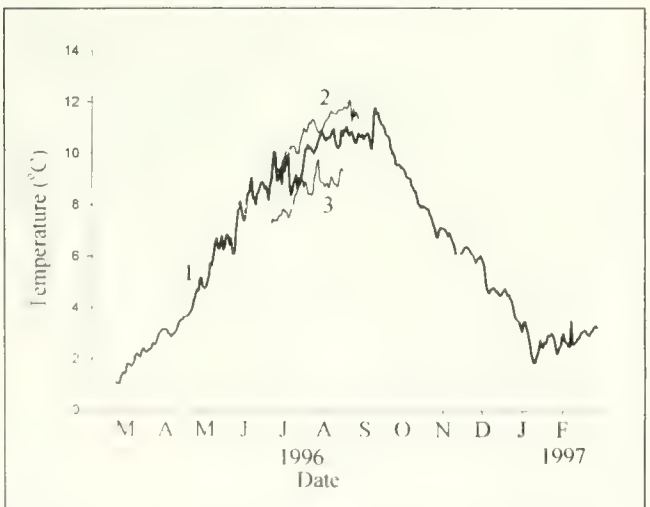

Figure 2

Seasonal variation in 1996 subsurface temperatures (5 m below low tide; 0 m = at Kachemak Bay (1), Chisik Island (2), and the Barren Islands (3).

Variability among consecutive beach seine sets and tidal states in Kachemak Bay

To assess variability in catches among sets and tidal states within Kachemak Bay, we made two sets immediately adjacent to each other at each site during consecutive high and low tides (i.e. 4 sets per site, 17 samples, 68 sets). CPUE declined markedly between first and second sets at both high (42% decline) and low (50% decline) tides, although numbers of species caught remained similar (Table 4). Jaccard's similarity coefficient for species composition indicated a high degree of similarity between the two adjacent high (75%) and low (74%) tide sets. However, species

diversity, richness, and evenness all increased on the second set, at both tidal states, because of a decrease in dominant species (Table 4). Because species composition of seine catches did not differ significantly between consecutive sets at high and low tidal states (Mann-Whitney rank sum test), it appears that one set is adequate for assessing species richness and dominance, as suggested by Allen et al. (1992)

Twenty-eight species were represented in high tide sets and the overall CPUE was 425, in contrast to 38 species and a CPUE of only 191 at low tide. This difference probably resulted from a scarcity of pricklebacks (Stichaeidae), gunnels (Pholidae), and sculpins at high tide. The species difference in catches in part accounted for the moderate coefficient of similarity (Jaccard's) between tidal states (58% and 61% on sets 1 and 2, respectively). Catch composition differed significantly between high and low tides (Mann-Whitney rank sum test; T=2645, P=0.02). Several schooling species (e.g. pink salmon, adult sand lance) and one demersal species (great sculpin) showed little disparity in overall CPUE or frequency of occurrence between tidal states (Table 5). These species (or age classes) appeared to remain close to the shore throughout the tidal cycle. Other species (e.g. Dolly Varden, juvenile sand lance) apparently moved from deeper waters into the intertidal zone at high tide, as shown by the greater frequency of capture and CPUE. Although Pacific cod, saffron cod, whitespotted greenling (*Hexagrammos stelleri*), silverspotted sculpin, juvenile great sculpin, and rock sole were caught at both tide levels, these species appeared to remain preferentially in the subtidal zone during high tide (Table 5). Overall, species diversity, richness, and evenness were greatest at low tides (Table 4).

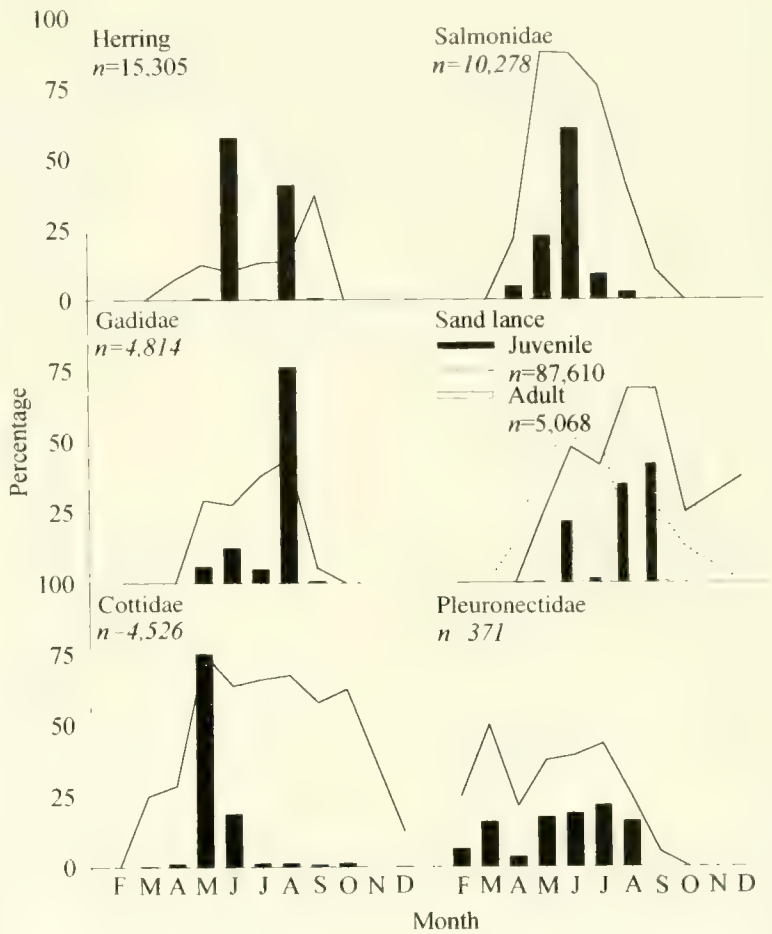

Figure 3

Seasonal variation in CPUE (bars) and frequency of occurrence (lines) of selected fish species caught by beach seines in Kachemak Bay.

Geographic comparison of beach seine catches from Kachemak Bay, Chisik Island, and the Barren Islands

A total of 988 fish representing 24 species were caught in 30 beach seine sets in the warmer (Fig. 2) nearshore waters around Chisik Island during summer 1996 (Table 6). Dolly Varden was the most common species; it was present in 63% of the sets and represented 30% of total catch by numbers. In contrast to Kachemak Bay and the Barren Islands, sand lance were found in only 33% of sets and accounted for only 24% of the catch by number. Snake pricklebacks (*Lumpenus sagitta*; 12%) and Pacific cod (8%) were the next most abundant species. Sculpins and flatfishes were also commonly caught in the sets.

A total of 180,232 fish representing at least 12 species (including 482 unidentified sculpins, 1 unidentified flatfish, and 1 unidentified greenling) were caught in 40 seine sets in the somewhat cooler (Fig. 2) nearshore waters at the Barren Islands during summer 1996 (Table 6). Barren Islands catches were dominated by sand lance (predominantly juveniles; Table 6). This species was found in 90% of the sets and represented over 99% of the total catch. Other species commonly found in the sets included Pacific

cod (>50%), sculpins (>40%), and butter sole (*Pleuronectes isolepis*; 18%).

CPUE varied by about two orders of magnitude among the three areas. On the basis of this variable, we determined that Barren Islands waters were more productive than those of Kachemak Bay and Chisik Island (Table 2). However, Chisik Island and Kachemak Bay displayed greater species diversity and richness than the Barren Islands (Table 2; Fig. 5). Equity (J') was much greater at Chisik Island (Table 2), indicating that this community was not dominated by any one species. Jaccard's similarity coefficients were low when compared between areas. Species assemblages in Kachemak Bay and at Chisik Island were similar (42%), and both of these areas differed from the Barren Islands (<25% similarity).

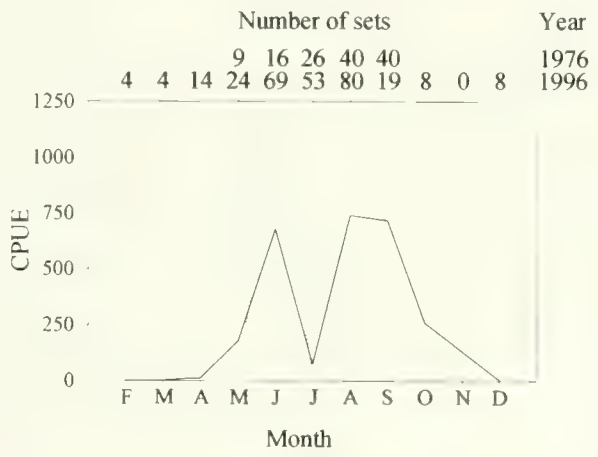

Figure 4

Seasonal variation of CPUE in beach seines during 1976 (·····) and 1996 (——) in Kachemak Bay.

Comparison of nearshore and shelf communities in lower Cook Inlet

In 1996, midwater trawls were made during July at all three study sites (Fig. 1). Nine species were found

Table 4

Catch-per-unit-of-effort (CPUE) and species diversity indices for consecutive beach seine sets made at high and low tides in Kachemak Bay. Diversity indices: H' = species diversity; D = species richness; J' = species evenness function (see "Methods" section).

Tidal state	Set	CPUE	Species	H'	D	J'
High	1	539.35	24	0.85	2.34	0.27
High	2	310.97	25	1.42	2.59	0.44
High	Overall	425.16	28	1.09	2.63	0.33
Low	1	255.26	33	1.96	3.53	0.56
Low	2	127.71	33	2.29	3.82	0.65
Low	Overall	191.49	38	2.17	3.91	0.60

Table 5

Frequency of occurrence and catch-per-unit-of-effort (CPUE) of selected fish species (occurring in more than 10% of sets) caught on consecutive beach seine sets made at high and low tide in Kachemak Bay.

	High tide				Low tide			
	Set 1 (34 sets)		Set 2 (34 sets)		Set 1 (34 sets)		Set 2 (34 sets)	
Species	% Occurrence	CPUE	% Occurrence	CPUE	% Occurrence	CPUE	% Occurrence	CPUE
Pink salmon	47.1	77.6	38.2	44.5	44.1	41.68	38.2	24.24
Dolly varden	47.1	3.09	47.1	14.85	29.4	1.65	32.4	2.26
Pacific cod	8.8	3.24	11.8	6.32	29.4	22.82	26.5	18.85
Saffron cod	5.9	0.06	2.9	0.74	14.7	4.88	14.7	7.82
Juvenile sand lance	44.1	417.94	61.8	187.32	32.4	88.97	32.4	9.79
Adult sand lance	35.3	8.74	32.4	16.4	41.2	24.76	38.2	2.00
Whitespotted greenling	8.8	0.15	2.9	0.03	20.6	0.32	23.5	2.06
Silverspotted sculpin	0.0	0.00	5.9	0.12	26.5	2.06	29.4	0.59
Juvenile great sculpin	8.8	5.88	5.9	15.24	26.5	46.59	23.5	33.74
Adult great sculpin	41.2	0.94	52.9	1.53	58.82	1.91	44.12	0.85
Tubenose poacher	2.9	0.03	2.9	0.09	8.8	0.18	11.8	0.32
Rock sole	2.9	0.03	11.8	0.12	58.8	3.32	50.0	2.59

(Table 7) that were not present in any of the beach seine sets (Tables 1 and 6). Similar proportions of the most abundant taxa were evident in trawl and beach seine samples from Kachemak Bay (Fig. 5), and sand lance dominated both nearshore and offshore catches. Few midwater trawls were made at Chisik Island because acoustic sign signals rarely indicated that fish were present in the water column. There was moderate overlap in composition of seine and trawl catches at Chisik Island, and no single species dominated the samples (Fig. 5). In contrast, the shelf environment of the Barren Islands was clearly dominated by walleye pollock, and nearshore habitats were almost completely populated by sand lance.

CPUE (defined as catch-per-individual-trawl) for trawl sets varied by an order of magnitude among the three study areas, paralleling results from beach seine sets (Table 2). Geographic trends in community diversity indices from trawl catches were also similar to those calculated for nearshore beach seine sets (Table 2). Species diversity (H'), species richness (D), and equity (J') were highest at Chisik Island, somewhat lower in Kachemak Bay, and lowest at the Barren Islands (Fig. 5).

Table 6

Frequency of occurrence and catch-per-unit-of-effort (CPUE) by species for beach seine catches at Chisik Island (30 sets) and the Barren Islands (40 sets) in 1996.

	Chisik Island (988 fish)		Barren Islands (180,232 fish)	
Common name[1]	% Occurrence	CPUE	% Occurrence	CPUE
Pacific sand lance	33.3	7.77	90.0	4465.03
Pacific cod	16.7	2.47	52.5	12.58
Dolly varden	63.3	9.90	2.5	0.13
Great sculpin	50.0	1.07	0.0	0.00
Pink salmon	13.3	0.70	35.0	11.23
Starry flounder	46.7	1.70	0.0	0.00
Unidentified sculpins	0.0	0.00	42.5	12.05
Snake prickleback	33.3	3.97	0.0	0.00
Capelin	13.3	0.43	10.0	3.38
Threespine stickleback	23.3	0.33	0.0	0.00
Butter sole	0.0	0.00	17.5	0.33
Rock sole	16.7	2.07	0.0	0.00
Lingcod	0.0	0.00	15.0	0.33
Whitespotted greenling	13.3	0.73	0.0	0.00
Crescent gunnel	10.0	0.37	0.0	0.00
Kelp greenling	0.0	0.00	7.5	0.13
Pacific herring	6.7	0.60	0.0	0.00
Eulachon	6.7	0.10	0.0	0.00
Silverspotted sculpin	6.7	0.07	0.0	0.00
Padded sculpin	6.7	0.07	0.0	0.00
Pacific staghorn sculpin	6.7	0.07	0.0	0.00
Sawback poacher	6.7	0.17	0.0	0.00
Rock greenling	3.3	0.03	2.5	0.03
Surf smelt	0.0	0.00	5.0	0.55
Coho salmon	3.3	0.03	0.0	0.00
Sockeye salmon	3.3	0.03	0.0	0.00
Longfin smelt	3.3	0.17	0.0	0.00
Pacific tomcod	3.3	0.07	0.0	0.00
Pacific halibut	3.3	0.03	0.0	0.00
Walleye pollock	0.0	0.00	2.5	0.03

[1] Latin names included in Table 1 except eulachon (*Thaleichthys pacificus*) and longfin smelt (*Spirinchus thaleichthys*).

Table 7

Total numbers of fish by species caught in midwater trawls in shelf waters within about 40 km of Gull Island (Kachemak Bay), Chisik Island, and the Barren Islands in 1996.

Common name	Scientific name	Kachemak Bay 16 Sets	Chisik Island 6 Sets	Barren Islands 17 Sets
Walleye pollock	*Theragra chalcogramma*	456	123	12,912
Pacific sand lance	*Ammodytes hexapterus*	3857	132	195
Capelin	*Mallotus villosus*	441	141	840
Pink salmon	*Oncorhynchus gorbuscha*	413	44	0
Pacific cod	*Gadus macrocephalus*	317	4	1
Pacific sandfish	*Trichodon trichodon*	0	59	0
Chinook salmon	*Oncorhynchus tshawytscha*	0	19	0
Tadpole sculpin	*Psychrolutes paradoxus*	16	0	0
Snailfish	*Cyclopteridae*	1	4	0
Eulachon	*Thaleichthys pacificus*	0	10	0
Prowfish	*Zaprora silenus*	9	0	1
Rock sole	*Pleuronectes bilineatus*	2	1	6
Flatfish	*Pleuronectidae*	6	0	0
Armorhead sculpin	*Gymnocanthus galeatus*	0	5	0
Sculpin	*Myoxocephalus* spp.	2	0	1
Sculpin	*Gymnocanthus* spp.	2	0	0
Dover sole	*Microstomus pacificus*	0	2	0
Poacher	*Bathyagonus* spp.	2	0	0
Smooth alligatorfish	*Anoplagonus inermis*	0	2	0
Pacific herring	*Clupea pallasi*	0	1	0
Spinyhead sculpin	*Dasycottus setiger*	0	1	0
Northern sculpin	*Icelinus borealis*	0	1	0
Ribbed sculpin	*Triglops pingeli*	0	1	0
Arrowtooth flounder	*Atheresthes stomias*	0	1	0
Starry flounder	*Platichthys stellatus*	1	0	0
Pacific lamprey	*Lampetra tridentata*	0	1	0
Total fish		5525	552	13,956

Discussion

Nearshore fish communities

The overall composition of beach seine catches did not differ between 1995 and 1996, and community indices were also similar between years. This gives us confidence that changes in community composition observed between 1976 and 1995–96 reflected decadal-scale variability rather than just annual variability. The increase in beach seine CPUE between 1976 and 1995–96 may have also been real, but we have less confidence in this result because beach seines were deployed closer to shore in 1976 (10 m) than in 1995–96 (25 m), and this difference might have influenced catch rates. The most dramatic difference between decades was in catches of gadids (including pollock). Few were caught in the whole of lower Cook Inlet during 1976, when gadids represented only 0.2% of the total catch (85 individuals in 262 seines; Blackburn et al., 1980). The 1000-fold increase in gadids that we observed in the mid-1990s parallels a similar increase in abundance of gadids in offshore shrimp trawls in Cook Inlet (Bechtol, 1997) and the Gulf of Alaska (Piatt and Anderson, 1996; Anderson et al., 1997). Similarly, the increase in pleuronectids and salmonids that we observed in Kachemak Bay between 1976 and 1995–96 was paralleled in the Gulf of Alaska in shrimp trawls (Anderson et al., 1997) and commercial salmon catches (Francis and Hare, 1994), respectively.

Interdecadal changes in abundance of these fishes are probably related to large-scale climate changes in the North Pacific, but causal mechanisms are unclear (Francis et al., 1998). Water temperatures in the northern Gulf of Alaska changed from being

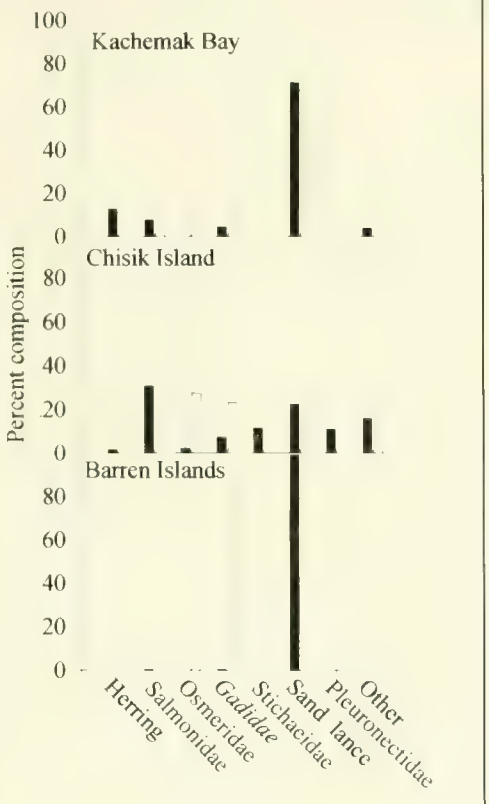

Figure 5

Species composition (% of total catch) in the nearshore (■) and shelf ( ) areas of Kachemak Bay, Chisik Island, and the Barren Islands.

colder than average through the 1970s to warmer than average through the 1980s and 1990s (Royer, 1993). Temperature changes have been linked to El Niño Southern Oscillation (ENSO) events and shifts in the location and intensity of the Aleutian low-pressure cell (Niebauer, 1983). This climatic "regime shift" caused a major reorganization of North Pacific biota (Francis et al., 1998). Phytoplankton and zooplankton abundance increased in the Gulf of Alaska, and this may have increased availability of food to larval stages of salmon and other groundfish, leading to enhanced recruitment (Francis et al., 1998). The timing of peak production of zooplankton biomass also changed, and this may have influenced recruitment in a suite of fish and invertebrates by altering the survival of larvae ("match-mismatch" hypothesis; Anderson and Piatt, in press). However, not all species appear to have been affected by changing climate. It is notable that the most abundant fish in Kachemak Bay, sand lance, exhibited no significant change in abundance or frequency of occurrence between 1976 and 1995–96. Sand lance have a unique life history. They spawn during the fall and larvae emerge in January or February, much earlier than the spring plankton blooms or larvae of many other Gulf of Alaska fish species. This strategy may be adaptive in situations where prey availability is unpredictable (Haldorson et al., 1993). Therefore, sand lance recruitment may have been little affected by changes in the timing or magnitude of zooplankton abundance during spring and early summer.

Capelin abundance declined sharply throughout the Gulf of Alaska after the late 1970s (Bechtol, 1997; Piatt and Anderson, 1996) but may have started to rebound in Cook Inlet waters during the early 1990s (Roseneau et al.[2]). Apart from catches in 10 beach seine sets (three sets in Kachemak Bay and at Chisik Island, and four at the Barren Islands), there is little evidence that capelin occur in nearshore areas of Cook Inlet. However, they were the third most common species caught in midwater trawls, and capelin were widely consumed by halibut and seabirds in Cook Inlet in 1995 and 1996 (Roseneau and Byrd, 1997; Roseneau et al.[3]). This species may occupy habitats offshore of the littoral zone, but largely inshore of where we made midwater trawls and may therefore be under-represented by this study.

The diversity of species in Kachemak Bay is comparable to that of other subarctic areas of Alaska. Isakson et al. (1971) caught 40 species in the nearshore waters of Amchitka Island and Orsi and Landingham (1985) found 42 species in southeastern Alaska. About 20–30 species are typically present in nearshore habitats in the more temperate regions of Sweden (Thorman, 1986a), Norway (Nash, 1988), Scotland (Gibson et al., 1996), and California (Allen and Horn, 1975; Horn, 1980; Allen, 1982).

In Kachemak Bay, four species accounted for over 92% of the catch in 1995–96, and two species represented over 93% of the 1976 catch. One species (sand lance) made up more than 99% of Barren Islands catch, and even at Chisik Island, where species equity was high, only five species accounted for 79% of the total numbers. As might be expected from these patterns of relative abundance, these fish were predominantly juveniles (Gibson et al., 1996) and typically low in the trophic web (Allen, 1982). In estua-

[2] Roseneau, D. R., A. B. Kettle, and G. V. Byrd. 1995 and 1996. Common murre restoration monitoring in the Barren Islands, Alaska. 1993 and 1994. Exxon Valdez Oil Spill Restoration Projects 93049 and 94039. Unpubl. final reports.

[3] Roseneau, D. G., A. B. Kettle, and G. V. Byrd. 1996 and 1997. Barren Islands seabird studies. *In* D. C. Duffy (compiler), APEX: Alaska Predator Ecosystem Experiment. Exxon Valdez Oil Spill Restoration Project. Alaska Natural Heritage Program, University of Alaska, Anchorage. Appendix J. Unpubl. annual reports.

rine, inshore, and bay habitats in the northeastern Pacific, it appears to be normal for five or fewer species to account for more than 75% of the individuals in local fish communities, even though the total number of species comprising these communities may be much larger (e.g. Allen and Horn, 1975; Hancock, 1975; Horn, 1980; Allen, 1982; Gordon and Leavings, 1984; Orsi and Landingham, 1985).

Although no significant differences were observed in species composition between consecutive beach seine sets at the same study sites, CPUE was markedly reduced for the second sets made at both high and low tides. This reduction in CPUE may have resulted from avoidance by schooling species to disturbance, or removal of most individuals during the first set. As Gibson et al. (1996) observed, we found marked differences in species composition between tidal states, and the number of species found at low tide was reduced by 26% in sets made at high tide. The fact that only species that typically migrate into the intertidal zone (e.g. pink salmon, sand lance, great sculpin) were caught at high tide may have accounted for this difference. Juvenile sand lance occurred in greater numbers and were caught at higher frequencies during high and flood tides, compared with low and ebb states as observed by Blackburn and Anderson (1997). These results suggested that juvenile sand lance may have moved laterally on each tide, by ascending from demersal habitats to pelagic zones at flood stages, and returning at ebb stages. Larval plaice *(Pleuronectes platessa)* of the North Sea exhibited this kind of behavior in coastal nursery areas (Rijnsdorp et al., 1985).

High-latitude fish assemblages, particularly those found in shallow water habitats, are subject to large seasonal variations in temperature and day length. These physical factors impart a strong natural seasonality to community structure (Nash, 1988) as observed in the nearshore waters of Kachemak Bay. Some fish species move from shallow water habitats to deeper waters in winter when thermal tolerances are exceeded (Allen and Horn, 1975; Allen, 1982; Bennett, 1989). Decreases in catch size between spring and fall peaks have also been observed by many investigators (e.g. Livingston, 1976; Horn, 1980; Allen, 1982; Thorman, 1986b; Methven and Bajdik, 1994). However, the midsummer CPUE declines in Kachemak Bay were not accompanied by declines in species diversity, as observed by Thorman (1986b). Reduction in numbers of adult Atlantic sand lance (*Ammodytes marinus*) has also been noted in midsummer seabird diets (Monaghan et al., 1996). This change corresponds to the time when predation by chick-rearing seabirds is at maximum; adult sand lance may be responding to the increased presence of predators by avoiding nearshore and surface habitats, or they may be coincidentally estivating in preparation for spawning (Sekiguchi et al., 1976).

Geographic variability

The relative abundance and distribution of fish species in lower Cook Inlet appears to be largely determined by oceanography and sediment influx. Intense insular upwelling of nutrient-rich waters around the Barren Islands leads to high productivity along frontal zones that in turn results in high abundance of fish. Upwelled water entering Kachemak Bay is nutrient-rich and becomes locally stratified, resulting in the highest primary production recorded in lower Cook Inlet (Larrance et al., 1977). In Kachemak Bay, high habitat diversity and the plankton prey-base provide the marine environments needed to support an abundant, diverse fish community. As water circulates around Cook Inlet to Chisik Island (Fig. 1), sediment loads increase from freshwater glacial runoff (Feely and Massoth, 1982), leading to maximum primary production that is only about one-tenth of that found in Kachemak Bay (Larrance et al., 1977). The lower abundance of sand lance at Chisik Island probably results from a combination of low food availability and deposition of glacial silt and mud (Feely and Massoth, 1982) that blanket most of the local substrates. Sand lance are known to require clean, sandy nearshore substrates (e.g. Pinto et al., 1984), and they appear to favor these habitats; few were caught in the offshore, oceanic waters surrounding the Barren Islands. On the north side of the Alaska Peninsula, sand lance also dominated nearshore catches and were caught less frequently offshore (Houghton, 1987).

The storm-prone Barren Islands displayed lower species diversity than the other lower Cook Inlet areas. Species inhabiting this more exposed oceanic region may avoid shallow habitats and favor slightly deeper, less disturbed waters (Thorman, 1986a), leading to reduced nearshore diversity (Horn, 1980). Diversity of fish in the nearshore Kachemak Bay and Chisik Island environments was apparently related to increasing habitat diversity and reduced salinity, as seen elsewhere (Thorman, 1986b; Blaber et al., 1995).

The most notable difference observed between nearshore and offshore shelf environments in lower Cook Inlet was that shelf areas were dominated by walleye pollock. Pollock were found in 88% of midwater trawls, compared with only 3% in beach seine sets. This species does not appear to use nearshore habitats as nursery areas, as does a related species, the Pacific cod (Houghton, 1987). The presence of some pollock in nearshore areas of Kachemak Bay may be related in part to the pres-

ence of oceanic water within the bay. Pollock also frequent Amchitka Island nearshore environments, which are similarly bathed by mixed, oceanic waters (Isakson et al., 1971).

Unequivocal declines in seabird populations (predominantly murres and black-legged kittiwakes) at Chisik Island (Slater et al., 1994) may be related to declines of locally abundant forage fish, particularly sand lance. It is possible that historically larger numbers of capelin (Piatt and Anderson, 1996) or herring (or both) (Rounsefell, 1930; Reid, 1971) may have inhabited this region when stocks of pelagic seabirds were higher prior to the mid-1970s. Colder than average temperatures prior to the late 1970s would have favored both of these fish species (Ware, 1995; Frank et al., 1996).

Limitations of the study

Sampling nearshore habitats with beach seines was limited to sandy and cobble substrates. Strong currents or inshore swells over 0.5 m also prevented effective retrieval of nets. Therefore, fish inhabiting muddy or rocky substrates, mussel (*Mytilus edulis*) and kelp beds, or the surf zone are under-represented in our study. The surf zone is preferentially used by some species because of low numbers of predators and food-rich waters (Bennett, 1989).

Burrowing fish, such as sand lance, may also be under-represented in the beach seine data because of their ability to escape under the net (Dick and Warner, 1982; Gordon and Leavings, 1984; Allen et al., 1992; Robards, personal obs). However, sand lance were the most abundant fish caught in Kachemak Bay and the Barren Islands, indicating that beach seines were clearly effective for sampling this species.

Juvenile cod migrate from deep water habitats during the day to shallower, nearshore waters at night (Methven and Bajdik, 1994; Gibson et al., 1996). Therefore, cod and other gadids may be under-represented in our catches, which were made only during daylight hours. However, diel variability in gadid catches has been shown to be lower than variability associated with tide cycles (Gibson et al.,1996).

Acknowledgments

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Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia

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Abstract.—Natural mortality was estimated for *Rhizoprionodon taylori* by using seven indirect methods based on relationships between mortality and life history parameters and one direct method, catch curve analysis. Estimated values from indirect methods were 0.60 to 1.65, whereas catch curves produced values of 0.56 for females and 0.70 for males. Demographic analysis was undertaken by using standard life history table techniques. Life history tables where each of the seven indirect estimates of natural mortality for *R. taylori* produced intrinsic rates of natural increase from −1.297 to 0.212 for an unfished population, and only two of the seven produced positive population growth. The implications of these results are discussed in relation to the accuracy of indirect methods for estimating natural mortality for *R. taylori* and other species of shark. The catch curve method was considered the best estimate of natural mortality and gave an intrinsic rate of increase of 0.27 and a doubling time of 2.55 years. The results of life history table analysis with the estimate of natural mortality from the catch curve analysis indicated that a *R. taylori* population could sustain fishing mortality up to 0.18 if applied evenly over all age classes, or 0.67 if age at first capture was two years. The implications of this study are discussed in relation to sustainability of elasmobranch stocks, particularly short-lived, fast growing, early maturing species.

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In a paper entitled "Problems in the rational exploitation of elasmobranch populations and some suggested solutions," Holden (1974, p. 137) concluded that "elasmobranch stocks offer very limited opportunities for long-term exploitation." Holden's conclusion was based on the fact that elasmobranch life history traits, such as slow growth, long lifespan, late age at maturity, and low fecundity, make populations very susceptible to recruitment overfishing. Holden's hypothesis has been supported by evidence from a number of shark stocks that have been rapidly overfished. These stocks include the spiny dogfish off Scotland and Norway (*Squalus acanthias*; Holden, 1968, 1977), the soupfin shark off California (*Galeorhinus galeus*; Ripley, 1946), the basking shark of the Irish Sea (*Cetorhinus maximus*; Parker and Stott, 1965), the porbeagle of the western Atlantic (*Lamna nasus*; Casey et al., 1978), and the sandbar and dusky sharks of the western North Atlantic (Musick et al., 1993). The majority of these examples are long-lived, slow growing, late maturing, temperate-water species. This group of commonly cited examples does not, however, represent the full range of elasmobranch life history traits and as such represents a biased set of data on which to base conclusions about sustainability of elasmobranch stocks. In particular, the examples lack representatives from tropical areas, especially short-lived, rapidly growing, early maturing species. With adequate information on species with a wide range of life histories, a more accurate assessment of the ability of elasmobranch stocks to sustain fishing pressure should be possible.

In recent years the use of demographic analysis (i.e. life history tables) has become popular in the assessment of elasmobranch populations and their ability to be sustainably fished (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Cortes and Parsons, 1996; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). This style of analysis requires only knowledge of the life history traits of a species. Because demographic models are static representations of populations with a stable age structure, they have limitations in respect to density-dependent responses (e.g. density-dependent natural mortality) and dynamic processes (e.g. fishing and variable recruitment) that can be included in dynamic models. The latter types of

Table 1

Methods used to estimate mortality for *Rhizoprionodon taylori* from life history parameter relationships. *GSI* = gonadosomatic index; K = von Bertalanffy growth parameter; L_∞ = von Bertalanffy growth parameter; M = natural mortality; T = average water temperature; t_{max} = maximum age; x_m = age at maturity; Z = total mortality.

Method	Relationships
Hoenig (1983)	$\ln(Z) = 1.46 - 1.01 \ln(t_{max})$
Pauly (1980)	$\ln(M) = -0.0066 - 0.279 \log(L_x) + 0.6543 \log(K) + 0.4634 \log(T)$
Gunderson (1980)	$M = 4.64\,GSI - 0.370$
Gunderson and Dygert (1988)	$M = 0.03 + 1.68\,GSI$
Jensen (1996) (age)	$M = \frac{1.65}{x_m}$
Jensen (1996) (growth)	$M = 1.5K$ (theoretical)
Jensen (1996) (Pauly)	$M = 1.6K$

models require abundance data (e.g. CPUE time-series data or fishery-independent surveys) that are not available for many elasmobranch populations. In cases where abundance data are not available, demographic models may represent the best available technique for the analysis of stock dynamics.

The Australian sharpnose shark, *Rhizoprionodon taylori*, is an ideal example of a small, short-lived, fast growing, early maturing tropical species (Simpfendorfer, 1992, 1993). It is endemic in the inner continental shelf waters of northern Australia between the Northwest Shelf and southern Queensland (Last and Stevens, 1994). It is captured throughout much of its range as bycatch in commercial fishing operations, including gillnet fisheries for barramundi, mackerel, and shark, and prawn trawl fisheries (Simpfendorfer and Milward, 1993; Last and Stevens, 1994). This paper reports the results of mortality estimation and demographic analysis for *R. taylori*. Mortality was estimated in two ways. First, a number of relations between mortality and life history parameters from the literature were used to evaluate the appropriateness of these methods for estimating natural mortality in sharks. Second, catch curve analysis was conducted to produce a direct estimate of mortality. The results of the demographic analyses are used to comment on the probable sustainability of short-lived, fast growing, early maturing, tropical elasmobranch populations.

Materials and methods

Estimation of mortality

Two approaches were taken to estimate mortality in *R. taylori*. The first was to employ relationships between life history parameters and natural mortality (M) or total mortality (Z) from the literature. Seven relationships were chosen (Table 1) to investigate variability in their results. All seven were based heavily on data from teleost fish, although most included some data from elasmobranchs. The most widely used relationship in elasmobranch studies is that of Hoenig (1983), which uses a linear function to estimate total mortality from maximum age. Although this method estimates total mortality, it was assumed to represent natural mortality for *R. taylori* because there was little or no fishing for this species in the study area (Simpfendorfer, unpubl. data). The method of Pauly (1980) uses two parameters of the von Bertalanffy growth curve (L_∞ and K) and average temperature to estimate natural mortality. Jensen (1996) reanalyzed Pauly's (1980) data and found that natural mortality could be estimated with the same level of accuracy based only on the value of K. In the same paper Jensen (1996) also gave two other relationships for estimating natural mortality based on life history theory, one based on K and the other on age at maturity. The final two relationships selected used maximum female gonadosomatic index (GSI) as an indicator of reproductive effort to estimate natural mortality. The method of Gunderson (1980) was based on only 10 species; Gunderson and Dygert (1988) expanded this to 20 species. Data for calculation of M were taken from Simpfendorfer (1992; GSI) and Simpfendorfer (1993; von Bertalanffy parameters, maximum age, and age at maturity).

The second approach to the estimation of mortality was catch curve analysis (e.g. Ricker, 1975; Vetter, 1987). Age data for the catch curves were taken from Simpfendorfer (1993). Ages were converted to whole years and the natural log of the number of individuals ($\ln N$) was plotted against age for males and females

separately. Mortality for each sex was calculated as the negative value of the slope of the regression line for points to the right of, and including, the peak ln N value. Ricker (1975) used only points to the right of the peak ln N value to calculate mortality; however, the small number of age classes in *R. taylori* meant that including the peak value would increase the reliability of the estimate. To confirm that the peak ln N value should be included in the regression calculations, linear and quadratic functions were fitted to the data. If the quadratic function provided a significantly improved fit as judged by an F test, then it was assumed that the inclusion of the peak ln N value introduced significant curvature into the data set and so violated the assumption of catch curve calculations that mortality is constant across all age classes. In this situation the peak ln N value was not used in the calculation. As with the Hoenig (1983) method, the estimate of mortality from the catch curves was taken to be natural mortality because there was little or no fishing pressure on the stock from which the age data were collected.

Demographic analysis

Demographic analysis of *Rhizoprionodon taylori* was undertaken with standard life history table methods (e.g. Krebs, 1985). The parameters estimated from the life history table were net reproductive rate (R_0), generation time (G), intrinsic rate of population increase (r), and population doubling time (t_{X2}). Positive values of r indicate that a population is able to replace itself and thus will not decline, whereas negative values of r indicate that the population is unable to replace itself and will decline. Values of r were calculated by solving the Euler equation (Krebs 1985):

$$\sum_{x=0}^{x_{max}} l_x m_x \cdot e^{-rx} = 1$$

where x = age;
x_{max} = maximum age;
l_x = the proportion of animals surviving to the beginning of a given age class; and
m_x = age-specific natality.

Age and growth data for the demographic analysis were taken from Simpfendorfer (1993). Maximum age was taken as 6 years for males and 7 years for females, and age at maturity for males and females was taken to be one year. Because Simpfendorfer (1993) was not able to validate age estimates (but did have supporting marginal increment and length-frequency data), sensitivity tests were run to investigate the influence of the uncertainty of age estimates (maximum age 10 years, age at maturity 2 years).

Reproductive data were taken from Simpfendorfer (1992). Litter size varied significantly with maternal length (Fig. 1; r^2=0.33, P<0.05). Because observations of litter size were made throughout the year, the litter size for each age class was calculated from the size of females at the midpoint of the age class. Mature females produce a litter each year. The sex ratio of the embryos was not significantly different from 1:1; therefore the litter size for each age class was halved to give the number of female pups per female. Although *R. taylori* matures at the age of one, the first litter is not produced until the end of the second year. Thus only females that survive to the end of that age class produce young. To accommodate this in the life history table, age-specific natality was calculated from the number of animals surviving to the end of a given age class (i.e. the number at the start of the next age class). Similarly, the age-specific natality of the final age class was set to zero because it was assumed that no animals survived to the end of the last age class. To assess the difference in results between calculating age-specific natality from the number present at the beginning and end of an age class, separate life history tables were constructed and the results compared.

A life history table was constructed for each of the values for natural mortality, calculated as described above, to investigate the sensitivity of demographic parameters to different values. To simulate increased mortality of the youngest age class, a number of other authors have doubled the normal value of M for the first age class (e.g. Hoenig and Gruber, 1990; Smith and Abramson, 1990; Cailliet, 1992; Sminkey and Musick, 1996). A life history table was constructed with double the normal value of M for the first *R. taylori* age class to test the sensitivity of outcomes to this approach.

Fishing mortality (F) was incorporated into the survivorship function of the life history table such that total mortality was the sum of M and F. The critical value of F, at which r equaled zero (i.e. the level of fishing beyond which the population could not replace itself, F_c), was calculated for each life table. For the calculation of F_c, fishing mortality was assumed to be equal for each age class. Negative values of F_c occurred when the population was declining without fishing and indicated that the population could sustain no fishing. The main source of fishing mortality on *R. taylori* in northern Australia is gill nets, which do not normally catch animals until they are at least one year of age. To investigate the effect of the age at which F begins (age at first cap-

Table 2

Life history table for *Rhizoprionodon taylori* based on various estimates of female natural mortality (M). R_0 = net reproducdtive rate; G = generation time; r = intrinsic rate of population increase; t_{x2} = population doubling time; F_c = level of fishing beyond which the population can not replace itself.

Scenario	Source of M	M	R_0	G	r	t_{x2}	F_c
A	Hoenig (1983)	0.60	1.547	2.235	0.212	3.273	0.140
B	Pauly (1980)	1.34	0.200	1.442	–0.869	–0.798	–0.600
C	Jensen (1996) (age)	1.65	0.096	1.301	–1.297	–0.534	–0.910
D	Jensen (1996) (growth)	1.52	0.130	1.353	–1.119	–0.619	–0.780
E	Jensen (1996) (Pauly)	1.62	0.103	1.312	–1.256	–0.552	–0.880
F	Gunderson (1980)	1.49	0.140	1.366	–1.078	–0.643	–0.750
G	Gunderson and Dygert (1988)	0.70	1.123	2.063	0.057	12.102	0.038
H	Catch curve (female)	0.56	1.758	2.304	0.271	2.554	0.179

ture, AAFC) the values of r at different levels of F and AAFC were calculated. F after AAFC was assumed to be constant across all ages.

Results

Mortality

The calculation of M from the various life history relations produced estimates ranging from 0.6 to 1.65 (Table 2). All the methods based on von Bertalanffy growth parameters gave results greater than one. Only the Hoenig (1983) and Gunderson and Dygert (1988) methods yielded estimates less than 1.

The length and age frequency data for *R. taylori* on which the age analysis of Simpfendorfer (1993) was based are shown in Figure 2. Estimates of M from the catch curves were 0.698 for males and 0.561 for females (Fig. 3). The first age class (0) for both males and females was excluded from the regression analysis to estimate M because it was lower than, and to the left of, the peak ln N value. Fitting of quadratic functions to the data did not significantly improve the fit to the data points selected (male: F=3.86, P=0.188; female: F=1.35, P=0.329), confirming that their inclusion did not violate the assumption relating to constant mortality.

Demographic analysis

Life history tables were constructed to obtain demographic results for the eight different estimates of M for an unfished *Rhizoprionodon taylori* population (Table 2). Three of the eight (A, G, and H) gave positive values of r: the methods of Hoenig (1983), Gunderson and Dygert (1988) and the catch curve method. The catch curve and Hoenig (1983) methods produced similar demographic results, with r values between 0.2 and 0.3, and with doubling times of 2.5 to 3.5 years (Table 2). These were considerably higher than for the Gunderson and Dygert (1988) method, which gave an r value of 0.057 and a doubling time of 12.1 years. The values of r for the remaining scenarios (B–F) were all much less than zero (–0.869 to –1.297; Table 2), indicating population decrease even with no fishing.

The value of M from the catch curve method was used to test the sensitivity of the life history table values to changes in model structure and age parameters. There was a large difference in age-specific reproductive rate calculated with a proportion of the

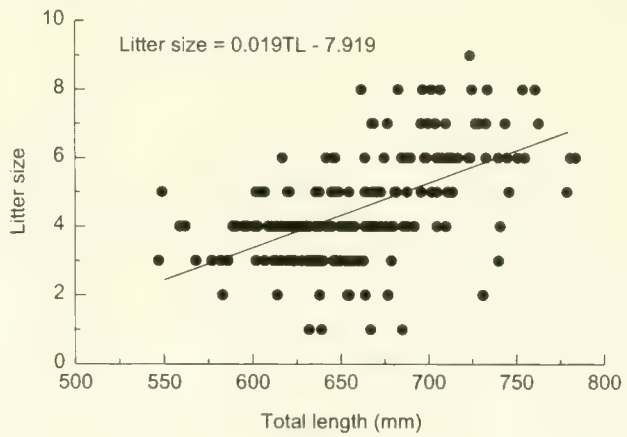

Figure 1

Litter size of *Rhizoprionodon taylori* as a function of maternal length. Data from Simpfendorfer (1993).

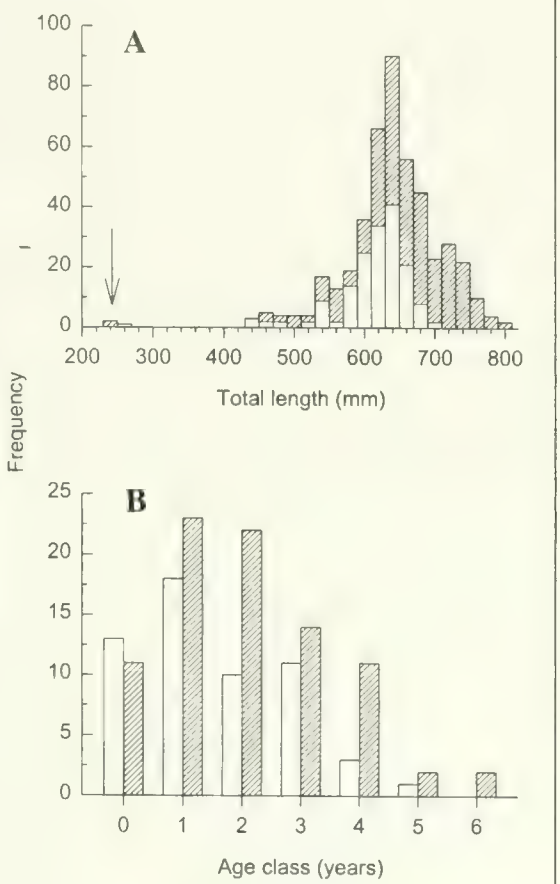

Figure 2

(A) Length and **(B)** age-frequency distributions of male (open bars) and female (hatched bars) *Rhizoprionodon taylori* from the waters of Townsville, Queensland. The arrow indicates size at birth.

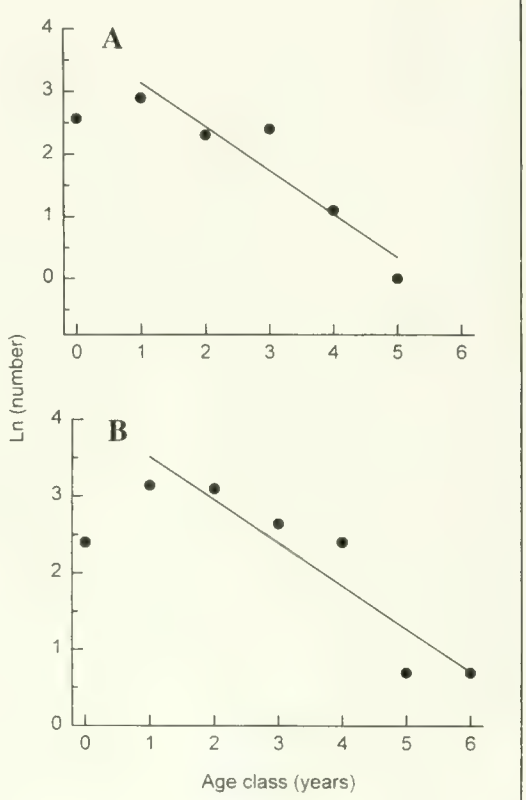

Figure 3

Catch curves for **(A)** male and **(B)** female *Rhizoprionodon taylori* derived from data from Simpfendorfer (1993). Data points for the first age class were not used to calculate regression lines.

population surviving to the beginning of an age class (J) rather than to the end (I). The value of r increased from 0.271 to 0.600, doubling time decreased from 2.544 years to 1.155 years, and the maximum value of F sustainable by the population (F_c) increased from 0.179 to 0.600 (Table 3) when the beginning of an age class was used. Doubling the value of M in the first year of life (I vs. K) caused a reduction in the value of r from 0.271 to 0.001, and population doubling time increased from 2.544 to 529.2 years (Table 3). The maximum level of fishing mortality that the population could sustain under such a scenario decreased from 0.179 to 0.001. Doubling first-year M and also calculating age-specific natality from the number surviving at the beginning of age classes (L) produced results identical to the base case (Table 3).

Increasing the maximum age to 10 years resulted in a small increase in r, from 0.271 to 0.276, and decreased population doubling time from 2.544 to 2.516 years (Table 3). Setting age at maturity at two years instead of one resulted in an r of 0.035, and a population doubling time of 19.82 years (Table 3).

Values of r varied considerably with changes in F and AAFC (Fig. 4). With an AAFC of 0, F_c = 0.18; with an AAFC of one, F_c = 0.27; and with an AAFC of two, F_c = 0.67. When AAFC was three or more the population was sustainable at F values up to at least 1.0.

Discussion

Mortality estimates

In most studies where natural mortality has been estimated for shark populations, particularly for use in demographic analysis, indirect estimation methods have been used (e.g. Hoenig and Gruber, 1990; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997). The results of the current study indicate that these indirect methods may provide a wide

Table 3

Sensitivity of life history tables to changes in model structure and age parameters. $l_{x+1}m_x$ indicates that age-specific natality was calculated from the number sharks surviving to the end of age classes; $l_x m_x$ indicates that age-specific natality was calculated from the numbers surviving at the beginning of classes; $2M_1$ indicates that natural mortality was doubled for the first age class; $1M_1$ indicates that natural mortality was constant for all age classes. Definitions of parameters are given in Table 2.

Scenario	Sensitivity test	R_0	G	r	$t_{\frac{1}{2}}$ (years)	F_c
I	Base case ($l_{x+1}\, m_x$, $1M_1$)	1.758	2.304	0.271	2.554	0.179
J	$l_x\, m_x$, $1M_1$	3.080	2.304	0.600	1.155	0.600
K	$l_{x+1}\, m_x$, $2M_1$	1.003	2.304	0.001	529.2	0.001
L	$l_x\, m_x$, $2M_1$	1.758	2.304	0.271	2.554	0.271
M	Maximum age = 10	1.820	2.488	0.276	2.516	0.183
N	Age at maturity = 2	0.035	3.061	0.035	19.82	0.026

range of estimates of natural mortality for a single population. Testing these values of natural mortality for *R. taylori* in life history tables showed that most of the methods produce values of r that would result in a population decreasing even when it was unfished. Such a result is biologically unreasonable. In contrast, Simpfendorfer (1999) made similar comparisons of indirect estimation methods for the dusky shark (*Carcharhinus obscurus*) and found that results did not differ greatly between methods. The difficulties in applying many of the indirect methods to *R. taylori* may relate to its short lifespan and fast growth because all but two of the methods used age or growth parameters to estimate natural mortality.

Among the indirect methods for estimating natural mortality, only those of Hoenig (1983) and Gunderson and Dygert (1988) yielded estimates that would allow an unfished population to increase. Although the values of natural mortality from the two methods were relatively similar (0.60 and 0.70, respectively), they produced different results when used in the life history tables to calculate r, with the Hoenig (1983) estimate producing a much higher value. This difference indicates that the results of demographic analysis are highly sensitive to changes in natural mortality. It is unlikely that the Gunderson and Dygert (1988) method produced a realistic value of natural mortality because it is based on the assumption that GSI is an index of total reproductive effort. Although this is true for most fish species, it is not the case for placental forms (such as *R. taylori*) in which much of the energy invested in reproduction is supplied during development rather than stored in the ovary prior to fertilization. Of the indirect methods used, the Hoenig (1983) method is therefore likely to be the most realistic estimate of natural mortality for *R. taylori*.

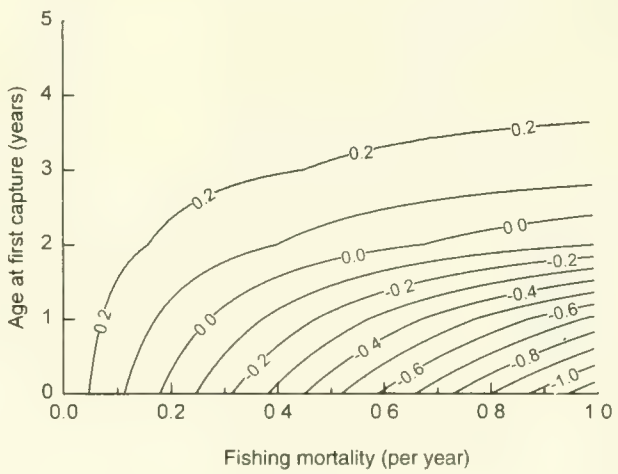

Figure 4

Contour plot of intrinsic rate of population increase (r) as a function of fishing mortality (F) and age at first capture (AAFC) for *Rhizoprionodon taylori* from northern Australia. Estimates are based on a life table where natural mortality was calculated by a catch curve (scenario H in Table 2). Fishing is sustainable at values of $r > 0$.

There are relatively few studies of shark populations in which natural mortality has been estimated directly with either tagging studies (e.g. Grant et al., 1979; Manire and Gruber, 1993) or catch curves (e.g. Cortes and Parsons, 1996). Although direct approaches to determining mortality would be expected to produce more realistic estimates, they must also meet a number of criteria in order to produce accurate results. The assumptions for the catch curve technique used in the present paper included constant mortality, recruitment, and selectivity over all age classes used in the calculations as well as random collection of samples from the population. The

data on which the calculations for *R. taylori* were based are likely to have met at least two of these assumptions. Because the area from which samples were collected was subject to little or no fishing, the population size should have remained relatively constant and thus fluctuations in recruitment would be minimized. The necessity of excluding the first age class from the catch curve analysis resulted from the selectivity of the gill nets used to collect specimens. For the age classes included in the analysis, the size of individuals was similar because growth rapidly reaches an asymptote, and therefore selectivity was probably reasonably constant. The assumption that mortality was constant was more difficult to test. However, the small size of *R. taylori* and the small change in its size after the first year or two of growth (Simpfendorfer, 1993) suggest that all age classes are likely to be subject to similar levels of predation.

The estimates of natural mortality for female *R. taylori* from the catch curve and from the indirect method of Hoenig (1983) were similar: 0.56 and 0.60, respectively. Such a finding is contrary to that reported by Cortes and Parsons (1996), who suggested that the Hoenig (1983) method would produce lower natural mortality estimates than those from catch curves. The present study suggests that for some species the Hoenig method will produce acceptable results. However, Cortes and Parsons' (1996) caution that demographic studies based solely on a natural mortality estimate from the Hoenig (1983) method should still be heeded because it is clear that the accuracy of this method may vary between species.

The most biologically plausible estimates of natural mortality for *R. taylori* (0.698 for males and 0.561 for females) are significantly higher than those reported so far for many other species of shark. Species with mortality levels of a similar magnitude are the bonnethead shark (*Sphyrna tiburo*) (0.625; Cortes and Parsons, 1996) and the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (0.42; Cortes, 1995). Each of these three species (*R. taylori, R. terraenovae,* and *S. tiburo*) are short-lived (6–12 yr). In longer-lived shark species, estimates of natural mortality are much lower. For example, Sminkey and Musick (1996) estimated an M of 0.105 for *Carcharhinus plumbeus*, which lives at least 30 years, and Smith and Abramson (1990), Cailliet (1992), and Au and Smith (1997) estimated that *Triakis semifasciata*, which lives to 30 years, has an M between 0.139 and 0.15.

The small size of *R. taylori* probably results in it being subject to high levels of predation throughout life. The small size at birth (220–260 mm) means that the first age class is particularly vulnerable to predation. The results of the sensitivity test, in which natural mortality was doubled for the youngest age class, indicate that this technique, which has previously been used to account for increased predation of young sharks, was not realistic for *R. taylori*. This is a result of the high value of natural mortality assumed for older age classes. It was not possible to estimate what, if any, increase in predation occurs for the youngest age class of *R . taylori*. However, any increase in predation would result in reduced estimates of r.

Demographic analysis

The most likely demographic results for *R. taylori*, those based on natural mortality estimated from the catch curve, indicate that the maximum value of r is about 0.27. This value is one of the highest for a species of shark. Cortes and Parsons (1996) estimated a similar rate (0.272–0.283) for *Sphyrna tiburo* from Florida with Hoenig's method to estimate natural mortality. *Rhizoprionodon taylori* and *S. tiburo* have similar life histories, with short lifespans, rapid growth, early maturity, and high natural mortality. All other published studies of shark demography have estimated intrinsic rate of increase at less than 0.1 (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). In most cases these species have been longer lived and slower to mature and have exhibited lower natural mortality than *R. taylori* or *S. tiburo*. The exception to this is *R. terraenovae*, which grows larger than *R. taylori* and is relatively short-lived (10 yr), but has a lower reproductive rate (Cortes, 1995).

Demographic analysis of *R. taylori* is sensitive to the way age-specific reproductive rate is calculated because of this species's short lifespan. Whether age-specific natality is calculated on the basis of the proportion of a population surviving at the beginning or the end of an age class leads to a very large difference in r. This effect is magnified by the high natural mortality of *R. taylori*. It is therefore important to take account of gestation period in the calculation of reproductive rate. This is less important in longer lived species in which natural mortality is lower and in which there is a relatively small difference between the proportions of a population surviving until the beginning and the end of an age class.

This study indicates that accurate age data are required for demographic analysis. The results for *R. taylori* showed a high level of sensitivity to changes in age at maturity, but only limited sensitivity to changes in maximum age. Given that the age data on which this research were based have not been validated, there remains some uncertainty about the results. Further work to validate these data (espe-

cially age at maturity) would decrease uncertainty. However, the length-frequency data supplied by Simpfendorfer (1993) support the hypothesis that *R. taylori* mature at age one and produce their first litter at age two.

Increasing age at first capture for *R. taylori* increased the level of fishing mortality that the population could sustain. Allowing individuals to remain unfished until they had produced one litter (AAFC=2) made fishing mortality levels up to 0.67 sustainable, whereas any level of fishing mortality was sustainable if individuals were allowed to produce two litters (AAFC=3). In a practical sense, AAFC restrictions are implemented as size restrictions. On the basis of the growth curves given by Simpfendorfer (1993), size of female *R. taylori* at the end of each of the first three years is 55, 67, and 71 cm total length (TL), respectively. The fact that size changes only slightly after the first two years makes the use of age restrictions unworkable for older individuals.

The gillnet fishery in which *R. taylori* is most often captured in northern Australian waters uses mesh sizes no smaller than 10 cm (stretched mesh). Gill nets of this size rarely catch animals less than 60 cm TL. The age at first capture in this fishery is therefore approximately one year. Although *R. taylori* less than one year of age are caught by trawlers, this fact was noted by the author only once in observations of research trawls between 1986 and 1992 in the Townsville region. On the basis that age at first capture of *R. taylori* in northern Australia is probably one year, demographic analysis indicates that the level of fishing mortality (F_c) that the population can sustain is approximately 0.27. However, Ricker (1975) showed that the level of fishing mortality needed to achieve maximum sustainable yield (MSY) is $r/2$. Thus for *R. taylori* $F_{MSY} = 0.135$.

Sustainability of fisheries

The comparison of demographic assessments of short-lived, fast growing, early maturing elasmobranch species such as *R. taylori* and *S. tiburo*, to those of longer-lived, slow growing, late maturing species indicates that they are likely to be able to sustain higher levels of fishing pressure than the latter species. For example, Sminkey and Musick (1996) reported that *Carcharhinus plumbeus* was most likely to be sustainable when $F_c \leq 0.1$, or $F_c = 0.25$ if a minimum size of 178 cm was used. Similarly, Cailliet (1992) reported that for *Triakis semifasciata*, $F_c = 0.084$ did not reduce the population, but that fishing mortality at double this level was sustainable only if animals 12 years and older were caught. This contrasts markedly with the results for *R. taylori* that the population may be sustainable at F_c=0.18, or F_c = 0.27 if age at first capture was one year. It is therefore possible that at least some species of elasmobranchs, in particular the shorter-lived, fast growing, early maturing species, are able to sustain limited commercial levels of fishing pressure. The apprehensive conclusion of Holden (1974) regarding sustainable fishing of elasmobranch stocks may need to be revised for selected species. However, the real challenge is to manage the development and regulation of such elasmobranch fisheries effectively.

Acknowledgments

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Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa

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Abstract.—The spotted gully shark, *Triakis megalopterus*, was sampled opportunistically over a 12-year period from catches of shore and ski-boat fishermen using hooks and lines. Most specimens (89.6%) were taken from rocky reefs less than 10 m deep, 8% were caught at 11–20 m, and only 2.4% were recorded from waters more than 20 m deep. The reproductive biology of 35 males and 87 females was examined. The spotted gully shark exhibits aplacental viviparity. Size at 50% maturity for males is ca. 1320 mm total length (TL) and for females ca. 1450 mm TL. Maximum sizes recorded here were 1520 mm TL for males and 2075 mm TL for females. Gestation appears to last 19–21 months. The female reproductive cycle may be 2–3 years, depending on the time between pregnancies. The sex ratio of embryos was found to be 1:1 but the postpartum male:female ratio was 1:2.5. Size at birth was estimated to be 420–450 mm TL. The smallest free-swimming individual recorded was 576 mm TL. Number of embryos per pregnancy ranged between 5 and 15, with a mean of 9.7. A total of 110 stomachs were examined in the feeding study. Diet changed with increase in shark size. Small sharks (<1 m) preyed mainly on Cape rock crabs, *Plagusia chabrus* (78% of mass), whereas sharks of 1–1.4 m preyed largely on Cape rock crabs (48%) and cephalopods (33%). Teleosts were more important for sharks larger than 1.4 m (54%); most of these prey were associated with rocky reefs.

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Fish. Bull. 97: 987–998 (1999).

The genus *Triakis* Müller and Henle, 1838, commonly called leopard shark, comprises small to moderately large, harmless, stocky sharks that feed on invertebrates and fish. *Triakis* is currently restricted to five species: *Triakis acutipinna* Kato, 1968 (sharpfin houndshark); *T. maculata* Kner and Steindachner, 1867 (spotted houndshark); *T. scyllium* Müller and Henle, 1839 (banded houndshark); *T. semifasciata* Girard, 1854 (leopard shark); and *T. megalopterus* (Smith, 1849) (sharptooth houndshark or spotted gully shark; Compagno, 1988).

Triakis megalopterus is a stout houndshark with a broadly rounded snout and a large mouth with small, pointed teeth. The head and body are gray or bronze above, usually with numerous small black spots, and white underneath (Bass et al., 1975). It is endemic to southern Africa (Compagno et al., 1989), where it occurs from northern Namibia, at about 21°45'S, 13°57'E, to Coffee Bay in Eastern Cape, South Africa, at 31°59'S, 29°09'E. The species is a common inshore bottom-dwelling shark of temperate continental waters, where it is caught by anglers in shallow subtidal waters. It prefers rocks and crevices in the shallows and is confined to water shallower than 50 m along the Cape coast (Bass et al., 1975; Compagno et al., 1989, 1991).

Very little has been published on the biology of this species (Bass et al., 1975). Although all five species of *Triakis* are viviparous, they lack yolksac placentas and the embryos obtain nourishment from their yolk sacs (Bass et al., 1975; Castro, 1983; Compagno, 1984; Kusher et al., 1992). Bass et al. (1975) and Compagno (1984) provided some information on the food habits of *T. megalopterus*, noting the presence of crabs (*Plagusia chabrus*), teleost fishes, and one small shark (*Scyliorhinus capensis*) in stomach contents.

At present, there is no scientific information that could guide management decisions on *T. megalopterus*, with the possibility of a small population size and limited range distribution (Compagno et al. 1989; Goosen, 1997), this species could be vulnerable to overexploitation in inshore multispecies shark fisheries. Off California, *T. semifasciata* has declined in abundance and consequently management measures have been proposed there (Smith and Abramson, 1990; Cailliet, 1992).

The aim of this study was to investigate the reproductive and feeding biology of *T. megalopterus*. Investigations of age and growth will be documented elsewhere. Improved knowledge of this species could underpin management strategies for this component of the multispecies shark fisheries off South Africa, which are known to be expanding (Smale, 1997).

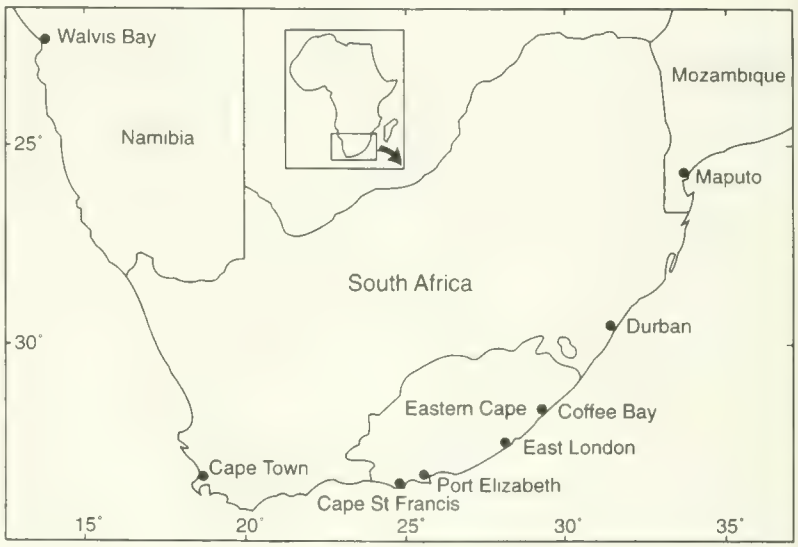

Figure 1
Southern Africa showing places mentioned in the text.

Materials and methods

Specimens were collected over a 12-year period, between February 1984 and October 1996, from catches made with hooks and lines by rock, surf, and skiboat fishermen. All specimens used in this study were collected along the Eastern Cape coastline between Cape St. Francis (34°12'S; 24°52'E) and Coffee Bay (31°59'S; 29°09'E), South Africa (Fig. 1). Specimens collected for biological sampling were examined as soon as possible after capture, or were frozen for later study. Sharks were measured to the nearest millimeter and, where possible, weighed with a spring scale accurate to 100 g. Measurements of total length (TL) can vary considerably depending on the placement of the caudal fin during measurement (Branstetter et al., 1987); in this study TL was measured on a horizontal line between perpendiculars, from the tip of the nose to the tip of the tail, with the tail at its maximum extension (Compagno, 1984). Total length is used throughout this paper, unless otherwise noted.

Reproductive information was collected for 35 males and 87 females. Maturity stages largely followed Bass et al. (1975), with minor modifications (Goosen, 1997). Each specimen was assigned to one of the reproductive stages: embryo, immature, adolescent, mature, and, in females, pregnant. The clasper was measured in length from the point of outside insertion in the pelvic fin to the tip of the clasper (CLO); from the point of insertion at the cloaca to the tip of the clasper (CLI); and in width at its thickest point (CBW) (Compagno, 1984). For females, the following data were collected: diameter of the two largest ovarian eggs, width of the oviducal gland, greatest width of the uterus, absence or presence of embryos and uterine eggs, and numbers of embryos and eggs if present.

Embryos were measured, sexed, and weighed. The mean length of embryos in each litter was calculated after abnormally developed individuals were excluded. Seasonality of mating, gestation period, and pupping season were examined by comparing embryo sizes in different months. Hepatosomatic indices (HSI) were calculated from the formula

$$HSI = (LW/BW) \times 100,$$

where LW = liver weight in grams; and
BW = total body weight in grams.

Stomach contents were examined as soon as possible after capture, or frozen for later analysis. Prey were identified to the lowest possible taxon. Excess liquid was drained off and the mass of the remains determined to the nearest 0.1 g on a top-loading pan balance. Bait used to capture the sharks was excluded from analyses.

Size measurements used for prey were carapace width (CW) in crabs, mantle length (ML) in cephalopods, and total length (TL) in teleosts and all other prey. After whole fish prey were measured, otoliths were removed to verify identification and paired, counted, and measured. Otoliths were used to identify well-digested prey and to estimate their length. Similarly, cephalopod beaks were collected, counted, and measured. Neither formalin nor alcohol was used to store stomach contents, because otoliths exposed to such preservatives become etched or brittle (Smale et al., 1995). Lengths of well-digested cephalopods and teleosts were determined from regressions relating beak and otolith lengths to body length (Smale, 1983; Smale et al., 1993, 1995). Digested otoliths had a chalky eroded appearance and were not measured for use in prey size estimates.

Diet was quantified by 1) frequency of occurrence (%F), the ratio of stomachs containing a particular prey to stomachs containing any prey, expressed as a percentage; 2) numerical importance (%N), the number of each prey expressed as a percentage of the total number of prey items; and 3) gravimetric importance (%M), the wet mass of a prey category as a percentage of the total weight of the stomach contents (Hyslop, 1980). By using all three methods of analysis, we avoided bias associated with the use of any one method (Hynes, 1950; Windell, 1968; Hyslop, 1980). No combination of methods was used because this may have resulted in combining sources of error (Berg, 1979). Reconstituted prey weights were not used because bias may have been introduced as a result of the different digestion and accumulation rates of fish otoliths and cephalopod beaks (Smale, 1983). Consequently, the actual wet mass of each item in stomachs was used to investigate prey composition in this study (Smale, 1991).

Preliminary analyses revealed considerable differences in prey between sharks of different sizes, and samples were subsequently divided into three arbitrary size classes: less than ≤999 mm, 1000–1399 mm, and ≥1400 mm TL. To investigate the relation between sizes of predator and prey, reconstructed prey lengths and masses were calculated with otolith and beak measurements. Recorded wet masses and carapace widths and lengths had to be used for crustaceans, and only intact crustaceans were included in the predator–prey size analysis. Common names used for crustaceans are after Holthuis (1991).

Results

Depth range

Material collected in this study was derived from fishermen exploiting a wide range of depths. Both shore-based and boat-based catches were sampled, although the proportion of effort in different depth ranges was not quantifiable. Nevertheless, *T. megalopterus* was taken mainly from shallow water. Of 125 specimens where collection depth was known, 89.6% were taken in shallow waters of 10 m and less. Only 8% were collected at 11–20 m and 2.4% at >20 m. The greatest capture depth recorded in this study was approximately 30 m, at an offshore bank. No obvious size-based habitat segregation was evident in this relatively small sample.

Size range and maturation

The overall male-to-female ratio in sharks sampled was 1:2.5. The smallest male and female sharks captured were 576 mm and 725 mm, respectively. Females attain larger sizes than males; the largest male sampled was 1520 mm, compared with the largest female of 2075 mm. The clasper length (CLI) of the smallest male was 43 mm and that of the largest (a male of 1402 mm TL) was 239 mm (Fig. 2A). Based on clasper size, degree of calcification, and presence of sperm in the seminal vesicle, maturation in these sharks begins at about 1210 mm and is complete at about 1369 mm (Fig. 2A). Claspers of one specimen of 1345 mm were not quite rigid but sperm presence was noted. The smallest mature male was 1250 mm and the largest immature male was 1196 mm. The claspers of adults measured, on average, 225 mm (range 205–239 mm, n=16).

Increase in the diameter of ovarian eggs indicates the beginning of maturation. Small eggs (<4 mm diameter) could be seen in the ovaries of females of 977 mm and larger. Egg diameter increased noticeably in specimens larger than 1460 mm (Fig. 2B). Mature females had yellow yolk-filled ova larger than 4 mm in diameter. The developing uteri appear as thin strips of translucent tissue with diameters of up to 2.5 mm in females smaller than 1365 mm. As maturation proceeds, the uterus widens first at its posterior end, becoming bottle-shaped at lengths of 1391–1405 mm, with a diameter of 4–16 mm at its widest part (Fig. 2C). One female of 1490 mm TL had a uterus width of 16 mm. All females over 1460 mm, except the previously mentioned individual, had uterus widths wider than 20 mm, and all adult females had uterus widths measuring 20–140 mm ($\bar{x}$=82.81, n=27). The oviducal gland was difficult to distinguish in the smallest females but usually measured between 3 and 7 mm ($\bar{x}$=5.64, n=14) in females of less than 1365 mm, and grows little until females reach 1460 mm (Fig. 2D). All females over 1460 mm had oviducal glands wider than 20 mm and all adult females, both pregnant and non-pregnant (resting), had oviducal glands measuring 20–51 mm ($\bar{x}$=31.7, n=29). The smallest pregnant female measured 1465 mm TL.

Reproduction

Of 48 sexually mature females sampled, 81% were pregnant. The number of embryos per litter ranged from 5 to 15 ($\bar{x}$=9.7, n=38). One female had 16 egg cases, but of these only 13 had normal embryos, one was empty, and two contained retarded embryos (length 6.5% of the next smallest embryo length). Considering the size of the female (1650 mm TL), it is possible that litters of up to 16 pups may be recorded. There is no significant difference in the number of embryos between left and the right uteri

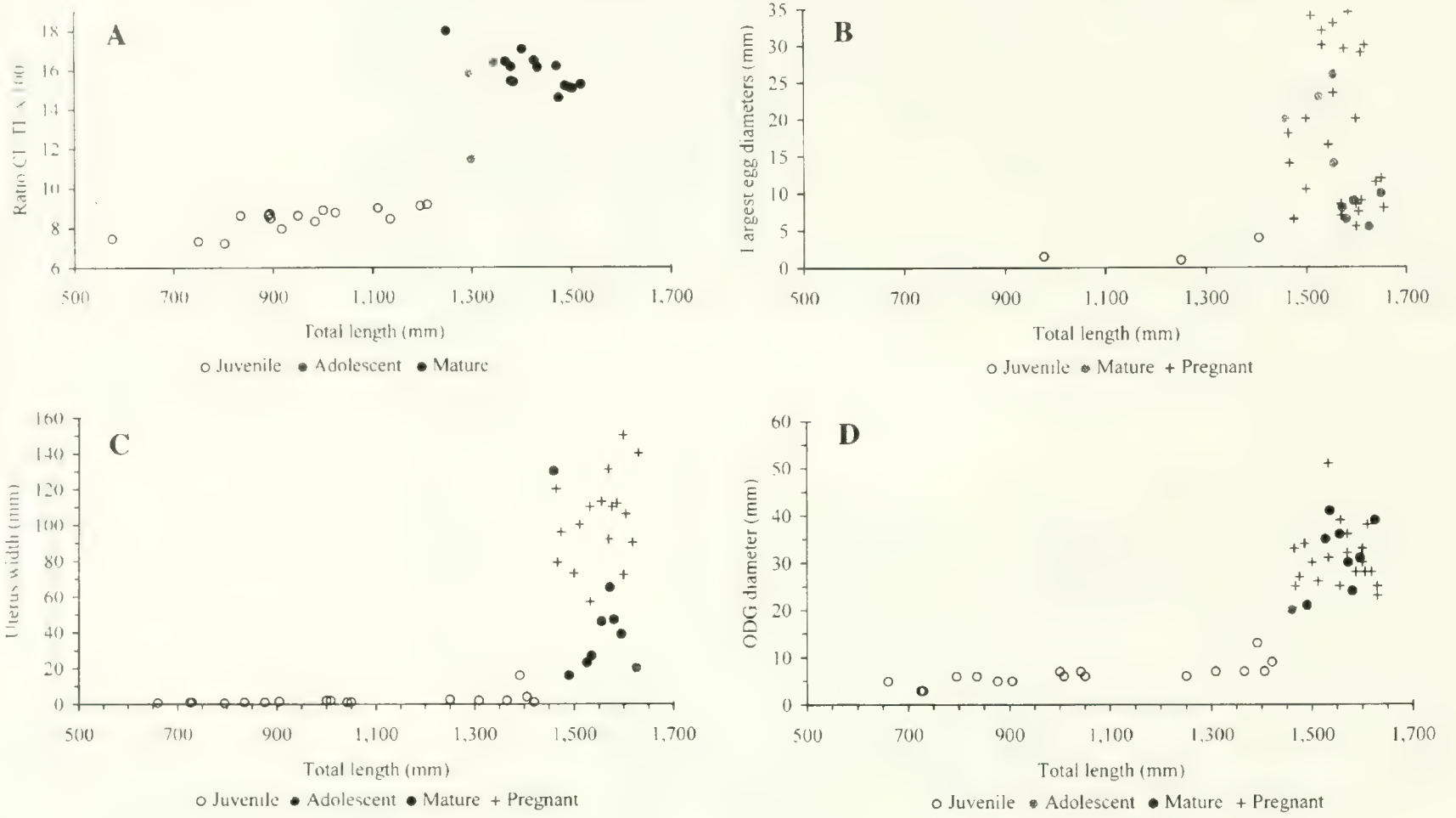

Figure 2

(A) Relation between inner clasper length (CLI) and total shark length, expressed as a percentage of total length. **(B)** Relation between diameter of the two largest ovarian eggs in each female and total length of female sharks. **(C)** Uterus width plotted against total length of female sharks. **(D)** Oviducal gland width plotted against total length of female sharks.

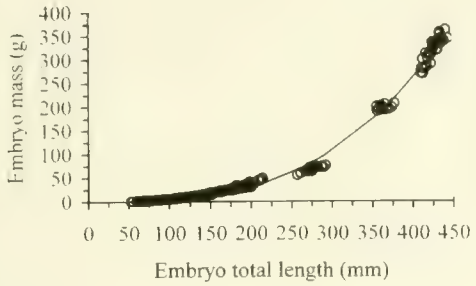

Figure 3

The relation between embryo mass (EM) and total embryo length (TL) was $EM = 2.397 \times 10^{-6} \times TL^{3.089}$ (r=0.99, n=275).

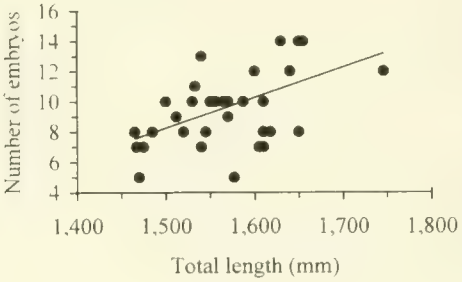

Figure 4

The relation between the number of normal embryos (n) and total length (TL) of pregnant females was $n = -21.74 + 0.020 \times TL$ (r=0.52, n=38).

(paired t test; P>0.5). Of the 244 embryos that were sexed, 122 were male and 122 were female.

The relation between wet body mass and total length of embryos was described by a power curve (Fig. 3):

$$W = 2.397 \times 10^{-6} \times TL^{3.089}, \qquad [r^2=0.994; n=275]$$

where W = embryo weight; and
TL = embryo total length.

Weight of near-term embryos ranged from 300 to 362 g ($\bar{x}$=331.4 g; n=23).

During all stages of development, the embryos within a uterus often differed in size; the largest embryos were as much as 30% longer than the smallest. Greater differences were found in early stages of embryonic development. Larger embryos usually occupy a more posterior position, suggesting that they are older than litter mates in more anterior positions. The embryos in both uteri were at equivalent developmental stages in all the samples. Embryo orientation within the uteri was normally head forward. Only two embryos from one batch lay head backward. Description of the developmental morphology of embryos was given by Goosen (1997).

Average observed embryo length in females between 19 May and 25 August was 425 mm (n=30). A female caught on 19 May had an embryo length range of 416–443 mm ($\bar{x}$=431 mm; n=15), whereas another female, caught on 25 August, had embryos in the length range of 412–440 mm ($\bar{x}$=425 mm; n=8). Yolk sacs were barely visible in the smaller of these embryos, and the largest had closed umbilical scars between the pectoral fins. Denticles and teeth of larger ones had erupted from the skin; one or two black spots were noted on some embryos. Their large size and eruption of teeth and denticles suggested that they had developed approximately to term. No embryo examined during this study showed any sign of a placental attachment between embryonic and maternal tissue. Embryos were readily removed from the uterus at all stages of development. Embryos are separated from each other in the uterus by enveloping uterine membranes, from which they apparently emerge shortly before birth. The largest embryo measured 443 mm and weighed 341 g. Based on available information, size at birth is estimated at 420–450 mm; birth probably occurs between May and August. The smallest free swimming individual, 576 mm in length, was taken in August.

Careful examination of embryos and uterine eggs showed that some of the uterine eggs failed to develop. Of 39 pregnant females, 11 (28%) had some nondeveloping uterine eggs. The greatest number of nondeveloping uterine eggs carried by a single female was 4 out of a total of 11, but most had only one or two. Of these pregnant females, 10 (26%) contained empty egg cases (no yolk). The largest number of empty egg cases carried by a single female was 12 (out of a total of 12). Occasionally, one embryo in a litter was deformed or retarded in growth. Because of the nondevelopment of a small proportion of uterine eggs, the number of developing, apparently normal embryos is a better measure of reproductive output than the number of uterine eggs. The relation between number of normal embryos and total length of the mother may be described by a linear regression (Fig. 4):

$$n = -21.74 + 0.02\,TL, \qquad [n = 38]$$

where n = litter size; and
TL = the total length of the mother in mm.

Litter size was found to be significantly correlated with total length of the mother ($P<0.01$, $r=0.52$, $n=38$).

The relation between shark length and liver mass was very variable but approximated a power relation (Fig. 5). The maximum recorded weight of females was about three times that of males; variation was higher in mature and pregnant individuals than in immature individuals.

To investigate the possible function of the liver as an energy source during pregnancy, female HSI was plotted against mean embryo TL (Fig. 6). Although the trend appeared negative, there was no significant correlation between mean embryo length and HSI ($r=0.242$, $P>0.05$; $n=31$).

Plotting mean embryo size against month of the year resulted in a scatterplot with two clusters of points but with no clear trend (Fig. 7). Extending the time axis to 24 months and shifting the larger embryos 12 months along the time axis yielded a clear trend. This finding would suggest that there is a gestation period of 19–21 mo and that the entire cycle spans approximately two years, excluding any resting period. Of a subsample of 11 mature females taken between May and August, four (36%) were resting (they showed no sign of recent pregnancy and had only small ova in the ovary) and the rest were pregnant, five (46%) with pups of intermediate size and two (18%) with large, near-term pups.

Feeding

A total of 110 stomachs were examined, consisting of 34 males (576–1520 mm TL) and 76 females (660–1746 mm TL). Females had a higher percentage of empty stomachs (20.5%) than males (12.1%). Preliminary analysis indicated a change in diet with predator size. This was investigated by grouping the data into three arbitrary size classes: smaller than ≥999 mm TL, 1000–1399 mm TL, and ≥1400 mm TL and longer. Prey taken clearly changes with increasing size (Fig. 8). Although invertebrates were important initially, larger sharks took more vertebrates (Table 1).

Small sharks fed almost entirely on crabs (Fig. 8). The Cape rock crab, *Plagusia chabrus*, dominated in the smaller two size classes of shark, in terms of mass (78.3% and 48.5%, respectively; Table 1). Larger crustacean taxa appeared in the diet of larger sharks. Cape slipper lobster, *Scyllarides elisabethae*, appeared in the second size class and Cape rock lobster, *Jasus lalandii*, and scalloped spiny lobster, *Pan-*

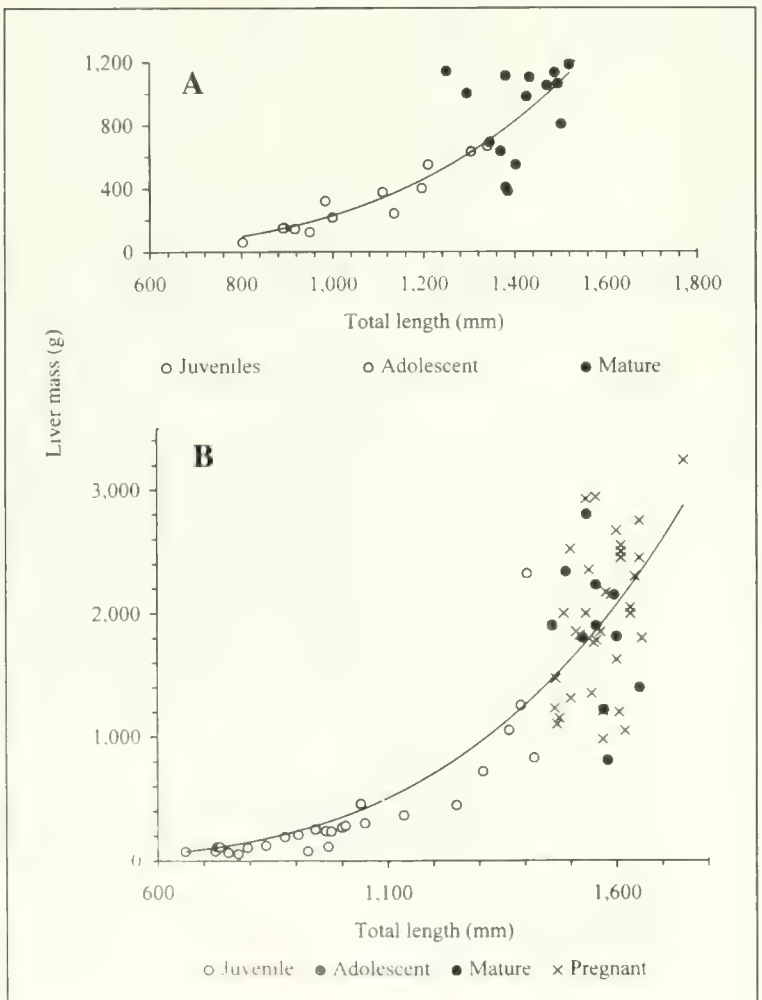

Figure 5

(A) The relation between liver mass (LM) and total length of male *T. megalopterus* was $LM = 9.517 \times 10^{-10} \times TL^{3.294}$ ($r=0.83$, $n=28$). **(B)** The relation between liver mass (LM) and total length of female *T. megalopterus* was $LM = 1.964 \times 10^{-9} \times TL^{3.152}$ ($r=0.86$, $n=73$).

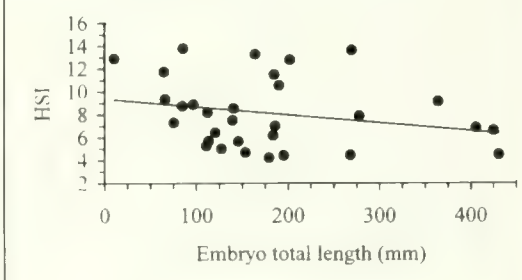

Figure 6

The relation between hepatosomatic index (HSI) of pregnant females and the mean length (TL) of normally formed embryos in the litter was $HSI = 9.376 - 0.0068\ TL$ ($r=0.242$, $n=31$).

ulirus homarus, appeared in the largest size class. Although crustaceans were important prey of the large sharks, they were less dominant in the diet.

Teleosts became more important prey for larger sharks. They included representatives from at least 10 families and 14 species (Table 1). They dominated the prey of large sharks by mass (53.9%) and by number (47%), whereas they contributed only 10.3% and 14.2% by mass for the medium and small-size classes, respectively (Fig. 8). Only three species of fish were eaten by the smallest sharks, of which barred fingerfin, *Cheilodactylus pixi*, was the most important. Six species were taken by the medium-size class, and twotone fingerfin (*Chirodactylus brachydactylus*) was the most important. The diet of the large-size class was dominated by several species, *viz.* seacatfish (*Galeichthys* sp.), cob (*Argyrosomus inodorus*), red tjortjor (*Pagellus bellottii natalensis*), and blue hottentot (*Pachymetopon aeneum*). The two largest teleost species ingested, based on recalculated total length, were a 336-mm sand steenbras (*Lithognathus mormyrus*) and a 334-mm seacatfish (*Galeichthys* sp.). Both were taken by sharks longer than 1500 mm TL.

Cephalopods were the second most important forage category for medium-size sharks (Fig. 8). The common octopus (*Octopus vulgaris*) and the squid *Loligo vulgaris reynaudii* were the most important species, making up 25.5% and 7.8% by mass, respectively. Cephalopods were minor prey for the largest class of sharks (4.6% by mass).

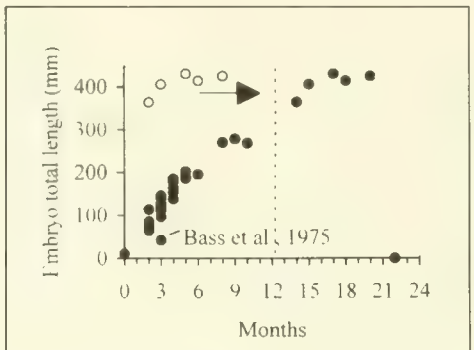

Figure 7

Mean size of normal embryos in each litter plotted against month of the year. The arrow indicates a shift of large litters (empty circles) to the same months one year later.

Elasmobranchs were relatively unimportant prey of spotted gully sharks. One stomach had the remains of a lesser sandshark (*Rhinobatos* sp.), another contained remains of a brown catshark (*Haploblepharus fuscus*), and two contained catshark eggs. The occurrence of anomalous food items was very rare. Inedible remains included a bryophyte (one stomach) and an unidentified mussel (one stomach).

In addition to ontogenetc variation in prey, prey size increased with growth (Fig. 9). Cape rock crab (*Plagusia chabrus*) was an important prey for sharks

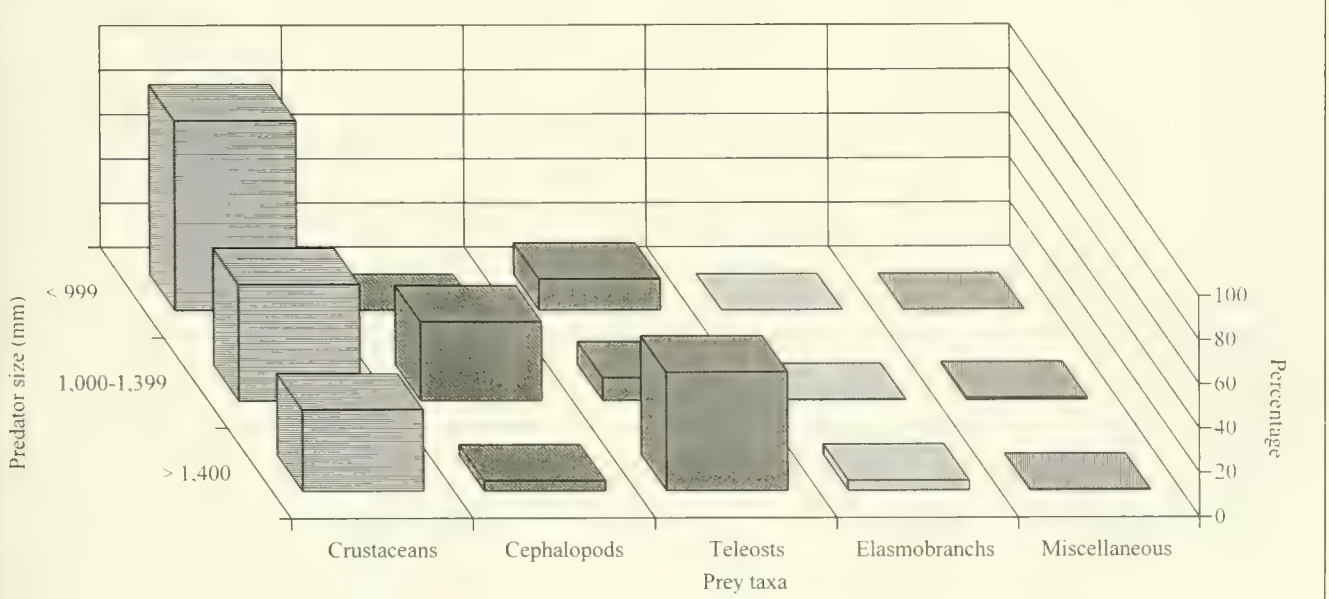

Figure 8

Percentage mass of different taxa in the diet for different size classes of *T. megalopterus*.

Table 1

Prey composition of three size groups of *T. megalopterus* from the Eastern Cape.

	< 999 mm TL			1,000–1,399 mm TL			> 1,400 mm TL		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
Crustaceans									
Atergatis roseus							2.38	1	1.63
Ovalipes trimaculatus	4	1.89	0.27	4	1.39	0.02	9.52	5	1.83
Plagusia chabrus	76	69.81	78.29	60	50	48.48	30.95	16	16.26
Jasus lalandii							2.38	1	6.65
Panulirus homarus							4.76	2	4.78
Scyllarides elisabethae				8	2.78	1.72	11.90	6	4.65
Caridea	8	3.77	0.06				2.38	1	0.11
Unidentified crab spp.	20	13.21	7.18	16	8.33	2.45	9.52	5	0.86
Molluscs									
Cephalopods									
Loligo vulgaris reynaudii				8	2.78	7.83	2.38	1	0.96
Octopus vulgaris				24	13.89	25.48	7.14	3	1.72
Sepia sp.							2.38	1	0.01
Gastropods									
Haliotis midae				4	1.39	2.51	2.38	1	1.90
Teleosts									
Ariidae									
Galeichthys sp.							11.90	6	13.10
Carangidae									
Trachurus trachurus capensis				4	1.39	2.32			
Cheilodactylidae									
Cheilodactylus pixi	8	5.66	13	4	1.39	0.07	2.38	1	0.45
Chirodactylus brachydactylus				4	1.39	3.98			
Gobiesocidae									
Chorisochismus dentex							2.38	1	1
Haemulidae									
Pomadasys olivaceum	4	3.77	0.79						
Mugilidae									
Liza richardsonii							2.38	1	0.94
Platycephalidae							2.38	1	0.01
Pomatomidae									
Pomatomus saltatrix							7.14	2	0.70
Sciaenidae									
Argyrosomus inodorus				4	1.39	0.93	4.76	4	8.50
Sparidae							4.76	2	0.01
Diplodus sargus capensis	4	1.89	0.40	4	1.39	0.50	2.38	1	0.10
Lithognathus mormyrus							2.38	1	3.37
Pachymetapon aeneum							4.76	6	4.65
Pagellus bellottii natalensis				4	1.39	1.92	4.76	5	5.25
Sarpa salpa							2.38	2	2.76
Unidentified teleost remains				16	5.56	0.61	30.95	14	13.02
Elasmobranchs							2.38	1	0.18
Scyliorhinidae							2.38	1	0.16
Haploblepharus fuscus							2.38	1	0.94
H. fuscus (egg cases)				4	2.78	0.28	2.38	2	0.31
Rhinidae									
Rhinobatos sp.							2.38	1	2.65
Skate sp. (egg case)							2.38	1	0.31
Miscellaneous									
Bryophyte							4.76	2	0.02
Unidentified mussel				4	1.39	0.86			
Tapeworm				4	1.39	0.03			
Unidentified material							2.38	1	0.20
Total[1]	25	53	1092.64	25	72	3,014.90	42	100	4,898.95

[1] Totals are numbers of stomachs with prey, number of prey items and prey wet mass in g.

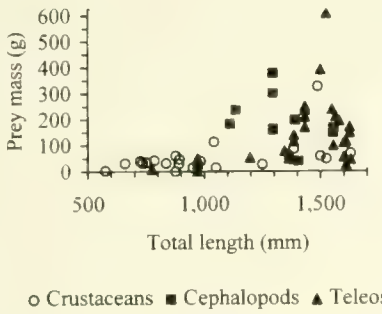

Figure 9

Calculated original prey mass plotted against *T. megalopterus* length, showing that the size of prey taken increases with predator size.

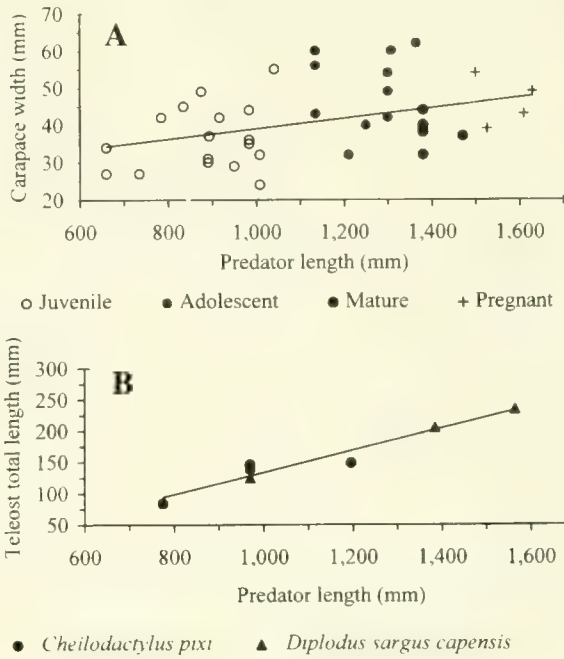

Figure 10

Relation between prey size and predator length. **(A)** *Plagusia chabrus* carapace width (CW) plotted against predator length. $CW = 25.1 + 0.014 \times TL$ (r=0.37, n=39). **(B)** Total lengths of two teleosts plotted against total length of the predator. The linear relation had the form TL (prey) = $-41.94 + 0.176 \times TL$ (predator) (r=0.97, n=7).

of a wide range of sizes, and there was a significant linear relation between crab carapace width and total length of sharks (r=0.37, P<0.05, n=39; Fig. 10A). Limited numbers of teleosts made analysis difficult. Combined data for two species (*Cheilodactylus pixi* and *Diplodus sargus*) showed a significant relation between the lengths of prey and sharks (r=0.97, P<0.01; n=7; Fig. 10B). The sample size of other prey species was too small to make similar analyses.

Discussion

Depth range

This study confirmed earlier reports that *T. megalopterus* prefers shallow rocky reefs (Bass et al., 1975; Compagno et al., 1989, 1991). They were found very rarely in deep waters, despite extensive sampling in deep waters for a variety of other sharks, including the closely related *Mustelus* species (Smale, 1991; Smale and Compagno, 1997). The nature of the samples precluded precise determination of intraspecific habitat choice, but there were no obvious differences in habitat choice by sharks of different sizes. The skewed sex ratio, which needs further investigation, may be due to sampling bias or social factors.

Reproduction

In *T. megalopterus*, eggs produced by the single functional ovary pass through the oviducal gland, where they are probably fertilized before they are enclosed in the membranous egg case. Embryonic development is ovoviviparous, embryos receiving nourishment from the yolk sac. However, some egg cases were slightly adherent and others intimately connected to the uterus wall. There was no evidence of the yolk sac forming a placental attachment at later stages of development, supporting Compagno's (1984) summary of the genus.

The size at which 50% of male sharks are mature is equivalent to mean size at maturity (Lenanton et al., 1990). Data from the present study indicated that males mature at approximately 1320 mm. Compagno (1984) estimated that males mature at 1300–1400 mm. On the basis of width of the oviducal gland and the diameter of the uterus and eggs, females begin to mature at about 1391 mm, and 50% maturity is achieved at about 1450 mm; all females larger than 1500 mm are mature. Compagno (1984) estimated that females mature between 1400 and 1500 mm and reported mature females of 1400–1740 mm. In this study, 50% maturity of female sharks is attained at about 1450 mm, which represents 70% of the maximum size observed, 2075 mm. This size falls within the range of 60%–90% noted by Holden and Raitt (1974). The smallest pregnant female measured 1465 mm.

Gestation in sharks is usually 10–12 mo and prolonged gestation periods are apparently rare, although *Squalus acanthias* has a gestation period of

22–24 mo (Wourms, 1977; Nammack et al., 1985; Hanchet, 1988; Wourms and Demski, 1993; Wourms, 1994). The gestation of frilled sharks, *Chlamydoselachus anguineus*, may be as long as three and a half years (Tanaka et al., 1990). The proposed gestation of about 20 mo in *T. megalopterus* is longer than the estimated 12 mo in *Triakis semifaciata* (Castro, 1983; Talent, 1985; Smith and Abramson, 1990). If the 20-mo estimate is correct, any females that mate shortly after parturition would have a resting period of two to three months. Some mature but nonpregnant females, however, show no sign of ovarian egg growth and development at the same time that others have large ovarian eggs or uterine eggs (or both) and small fetuses. These resting females represented 36% of the sample of 11 mature females taken between May and August. These females probably skip a year and have an extended reproductive break of at least 12–15 mo, which would prolong the cycle to at least 3 years for some individuals. On the other hand, some pregnant females about to undergo parturition have large ovarian eggs, and these individuals may mate within a few months and apparently forego the extended resting period.

On the basis of embryo growth rates presented above, mating and fertilization probably occur from about October to early December. Females carry term embryos of 422–440 mm (largest embryos) between the last week of May and the last week of August, which would approximate the time of parturition. Compagno's (1984) estimate of size at birth was much smaller (300–320 mm) than that of our findings. From observations of embryonic development, it was noted that during the late stages of embryo development (from ca. 400 mm), both external and internal yolks were absent. The small amount of yellow substance in the spiral valve was thought not to be an internal yolk reserve, but the area of absorption. It was also noted that each embryo was contained in a soft egg case with ca. 500 mL of fluid (Goosen, 1997). Wourms and Demski (1993) noted that in *Squalus acanthias*, several months into the 22-mo gestation period, embryos can ionoregulate and osmoregulate in a uterine solution resembling seawater. This might be the case for *T. megalopterus* and could contribute to near-term embryo nourishment until parturition occurs.

The liver mass of a shark is a good index of the shark's condition (Springer, 1960). In our study it was found to fluctuate widely, particularly after maturation. Seasonal variation in HSI of the lesser sandshark (*Rhinobatos annulatus*) has been attributed to fluctuations in lipid content of the liver, which has been correlated with reproductive condition in females (Rossouw, 1987). Similar changes in HSI have been recorded in pregnant females of three *Mustelus* species (King, 1984; Smale and Compagno, 1997). Although low HSI values were found in pregnant females with near-term embryos in this study, the relation was not statistically significant, possibly suggesting that HSI fluctuates with other physiological factors. These observations were based on a small sample size and need further investigation.

Feeding

This study showed that *T. megalopterus* changes diet with growth, which suggests that it selects prey of suitable size. Because there is no evidence to date of marked habitat change with growth, and all sizes of shark do not have the same prey, it is unlikely that they are feeding opportunistically, even if they favor abundant species. Opportunistic feeding *sensu* Wetherbee et al. (1990) implies that stomach contents are varied but of composition and abundance similar to those of prey in the environment. Smale (1996) noted that the term "opportunistic" should be used with caution because it is difficult to distinguish between abundance and availability. Ontogenetic variation in feeding of *T. megalopterus* appears to be attributable to broadening the diet to include more energetically rewarding species (e.g. teleosts), although benthic prey are still taken.

Spotted gully sharks fed primarily on the crab *Plagusia chabrus*; as sharks grew, larger individuals were taken. This finding conforms with those where large crabs were taken by larger leopard sharks (*T. semifasciata*; Talent 1976). Although spotted gully sharks are most abundant near reefs, they may also hunt over sandy areas to exploit the crab *Ovalipes trimaculatus*, which prefers sandy substrates. Spotted gully sharks preyed largely on nocturnally active lobsters (Paterson, 1969; Smale, 1978; Zoutendyk, 1988) and crabs (Brown, 1961; Warner, 1977), suggesting that they are nocturnal hunters that take crustaceans as they emerge. Such activity may explain why anglers catch them more frequently at night.

As the sharks increase in size, they use a much wider variety of prey groups, including teleosts. Therefore, with growth the spotted gully shark is able to attack and ingest larger prey species. Nocturnally hunting sharks may be able to take some teleosts when they are less active or resting at night. Elasmobranchs became increasingly important prey with growth, a finding that supports previous observations of congeners taking elasmobranchs (Bass et al., 1975; Russo, 1975; Talent, 1976; Compagno, 1984).

Octopus vulgaris was the most common cephalopod prey. It inhabits reefs (Smale and Buchan, 1981; Roper et al., 1984) and emerges from its den to hunt

between dusk and dawn (Smale and Buchan, 1981), making it vulnerable to nocturnal predators. Squid (*Loligo vulgaris reynaudii*) is common throughout the Agulhas Bank (the continental shelf between Cape Town and Port Elizabeth) but become concentrated inshore in spring and early summer, when it spawns (Sauer and Smale, 1991; Augustyn et al., 1992). Egg laying is concentrated on the bottom during the day in waters 10–50 m deep (Augustyn, 1990; Sauer et al., 1997). Squid are thought to be especially vulnerable to predation during mating and spawning (Smale, 1991; 1996). Sauer and Smale (1991) recorded *T. megalopterus* as one of the squid predators in the vicinity of spawning aggregations, which illustrates its ability to exploit a superabundant prey resource by day, even though it normally appears to hunt at night.

In conclusion, it is evident that the habitat preferences of gully sharks make them vulnerable to exploitation by inshore fishermen. Their life history traits—large size at maturity, prolonged gestation period, and relatively small litter size—suggest that this species is unsuitable for sustained harvesting by either recreational or commercial fishing.

Acknowledgments

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Behavior of winter flounder, *Pseudopleuronectes americanus*, during the reproductive season: laboratory and field observations on spawning, feeding, and locomotion

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Abstract.—Continuous observations in a large research aquarium (121 kL) over a 14-week period were combined with field collection in the Navesink River estuary, New Jersey, to explore the behavior of winter flounder (*Pseudopleuronectes americanus*) during and after the spawning season. Ten males and ten females held in the aquarium spawned over a 60-day period, with an average of 40 spawns per female and 147 spawns per male. Males initiated all observed spawning events, which occurred throughout the night, but primarily between sunset and midnight. Spawning by one pair frequently elicited sudden convergence and spawning by secondary males (up to six individuals); consequently, strictly paired spawning was uncommon (22% of events). Males and females were almost entirely nocturnal during the reproductive season but became increasingly diurnal during the postspawning season.

Males and females arrived in the estuary in ripe spawning condition; fish with high gonadosomatic indices were collected during most of February and March 1997. All of the ripe females were >20 cm in total length and at least two years old, whereas ripe males measuring 10–15 cm were common. Ripe males were found throughout the system whereas ripe females were concentrated in the middle reach of the estuary. Field collections revealed that females began feeding, primarily on ampeliscid amphipods and on siphons of the clam *Mya arenaria* earlier in the season than males. Males in the laboratory also began feeding late in the season, after most spawning had ended. Field and laboratory results combine to indicate that male spawning strategy is adapted to maximize numbers of eggs fertilized. There is probably high genetic diversity in the offspring from any one female owing to frequent spawning and to multiple males participating in individual spawning events.

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Winter flounder, *Pseudopleuronectes americanus*, is an important commercial and recreational fishery species in estuarine and continental shelf habitats along the Atlantic coast of North America from Labrador to Georgia (Scott and Scott, 1988). A large number of investigations have been devoted to this species and its life history is relatively well known (Klein-MacPhee, 1978; Able and Fahay, 1998). Winter flounder populations include several substocks that mix during summer residence on the shelf, but adults return to natal estuaries to spawn (Saila, 1961; Poole, 1966; Howe and Coates, 1975; Pierce and Howe, 1977; Phelan, 1992). In the Mid-Atlantic Bight, adults make seasonal migrations into the estuaries of New York and New Jersey (Perlmutter, 1947; Phelan, 1992) where they spawn in shallow inshore waters during late winter (Scarlett and Allen, 1992).

Winter flounder in the mid-Atlantic region are believed to mature at 2–3 years, at 20–25 cm total length (Perlmutter, 1947, Danila, 1978; Witherell and Burnett, 1993). Considerable attention has been given to seasonal movement (Perlmutter, 1947; Saila, 1961; Howe and Coates, 1975; Phelan, 1992) and to fecundity and reproductive state in wild populations (Kennedy and Steele, 1971; Danila, 1978; Burton and Idler, 1984; Nelson et al., 1991); however, information on spawning behavior is limited to observations made by Breder (1922) of fish in small laboratory tanks.

In this investigation we expanded Breder's (1922) description of spawning and courtship in winter flounder by making continuous observations on a population of winter flounder in a large research aquarium for a 14-week period during and after the reproductive period. We determined the total number of spawning events for males and females in the population and examined seasonal and diurnal variation in spawning, feeding, and locomotory activity. On the basis of field collection we described population structure, gonadal development, feeding, and localized movements by a wild population of winter flounder in an

estuarine spawning ground during winter and spring 1997.

Methods

Laboratory observations

Experimental animals Winter flounder were collected in nearshore waters between Rockaway Point and Coney Island, New York, on 27 January 1997 with a 9.2-m otter trawl fished from RV *Gloria Michelle*. Flounder were held in live cars with flow-through seawater and transported in large ice chests to the laboratory. Mature ripe males were identified by the extrusion of sperm under light pressure applied to the body. Females were identified by the presence of full ovaries distending the body, occupying a large portion of the body cavity, and extending almost to the caudal peduncle. Ten males and ten females, each greater than 200 mm in TL (total length), were marked with Peterson tags (13 mm diameter) before release into the research aquarium. To provide visual identification of gender on videotape, males and females were marked with orange and white tags, respectively. These colors were distinguishable with low-light video cameras during both day and night. At the beginning of the experiment the mean total length of male flounders was 29.8 cm (SD=3.2, range=24.3–34.4 cm). Mean length of females was 28.5 cm (SD=2.6, range=23.5–30.8 cm). Four fish (two males and two females) died near the end of the 14-week observational period; these were not replaced. The fish were remeasured for total length at the end of the experiment to estimate growth.

Research aquarium Observations of the winter flounder were made in the research aquarium at the James J. Howard Marine Sciences Laboratory at Sandy Hook, New Jersey. The aquarium (121 kL volume) is an oval 10.6 m long, 4.5 m wide, and 3 m deep, with eight rectangular windows (0.7 m wide and 1.2 m high), one in each end and three along each side. There is a recirculating system so that 10% of the water is replaced each week. Seawater upwells through coarse sand which covers the bottom of the aquarium (46 m^2) to a depth of 40 cm, then exits through drains at the top of the tank.

For this experiment, photoperiod in the aquarium room, which was controlled by a computer-driven bank of fluorescent lamps (Duro-Test, Vita-Lite: model CRI91; 5500°K), was programmed to follow the natural sequence at the location of the laboratory (40°28'N, 74°00'W), with a 13.5-h dark period at the end of January, when fish were first introduced into the system, and a 10-h dark period at the end of the study in mid-May. During nighttime hours, light intensity on the sediment surface was 0.17 lux (1.98×10^{-6} mEinsteins PAR [photosynthetic active radiation]). Light intensity increased at the time of twilight to 2.0 lux (2.92×10^{-5} mEinsteins PAR) for 20 min, followed by a natural rise in intensity to 206 lux (0.0027 mEinsteins PAR) at midday. Return to nighttime conditions followed an exact reverse pattern.

Water temperature was held at 4.0°C (±0.5°C) from the beginning of the observations until 27 March, when a cooling system malfunction allowed temperature to rise to 7.5°C. To follow conditions in the Navesink River, we held water temperature at 7.5°C until 10 April, then raised temperature ~0.5°C per day to 15°C on 14 April. This temperature was maintained until the end of observations on 13 May 1997.

Finely chopped pieces of frozen surf clam (*Spisula solidissima*) were made continuously available as food for the flounders. The food was renewed at least once per week during the early part of the period when feeding was light, and increased with ingestion rate to near-daily additions by 1 April 1997. The food was placed on the bottom in an area approximately 2 m in diameter within camera view so that all feeding bouts could be counted.

Recording observations Two low-light-sensitive video-tape cameras were set at the end windows of the aquarium to make continuous recordings of courtship and spawning events over a large portion of the tank from bottom to water surface. Each of these cameras viewed 53% (24.6 m^2) of the tank bottom with minimal overlap in coverage. Recordings were made from about 1530 h through 0500 h between 29 January and 18 April 1997, after preliminary taping and routine visual observation indicated that virtually all activity was nocturnal. The validity of this approach was confirmed by cameras at the side windows set for 24-h recording throughout the study period. Twenty-four-hour recording from the end cameras was initiated 19 April 1997, concurrent with increasing daytime activity of the fish.

Spawning events were divided into two classes. An event was considered "definite" when characteristic behavior patterns were clearly observed in the recorded image. However, because most spawning occurred in darkness, some spawning events were not observed clearly. These likely but less certain spawning events were scored "probable." Two forms of courtship were recorded; these are described in the "Results" section. Records were kept of the numbers of males and females involved in each courtship and spawning encounter. A feeding event was scored once,

regardless of feeding duration, when a fish entered the food distribution area and made obvious feeding motions toward the clam pieces. Analysis of video tape from the two cameras for four dates during midspawning season revealed that there were no significant differences in daily counts of spawning, courtship, and feeding as recorded by the two cameras (paired-sample t tests, $P>0.30$); therefore, the second camera was used only as a backup for recorder failure (e.g. on four dates).

Two other low-light cameras were set at side windows to provide data on locomotory activity and swimming speeds. Each viewed a 3.6-m wide section of the opposite tank wall and about 4.6 m^2 of bottom, and recordings were made for 5 min at the beginning of each hour. An index of locomotory activity was provided by the number of fish passing a central line in view of the camera. Swimming speeds (cm/sec) were determined by timing the passage of fish between two points 142 cm apart on the tank wall. Whenever possible, the gender of fish passing through this view was noted. The two cameras provided essentially identical information, and recordings from only one were analyzed for each day.

Observations were also made on the relative abundance of winter flounder larvae in the aquarium. Flounder larvae were almost constantly present in the aquarium after mid-February, and an index of their abundance was recorded each day. Because the larvae demonstrated diurnal vertical migration, observations were made at approximately 1200 h and general abundance was scored from zero to four. A score of one was recorded when only a few larvae were observed in any field of view and a score of four was given when thousands of larvae were present at all of the tank windows.

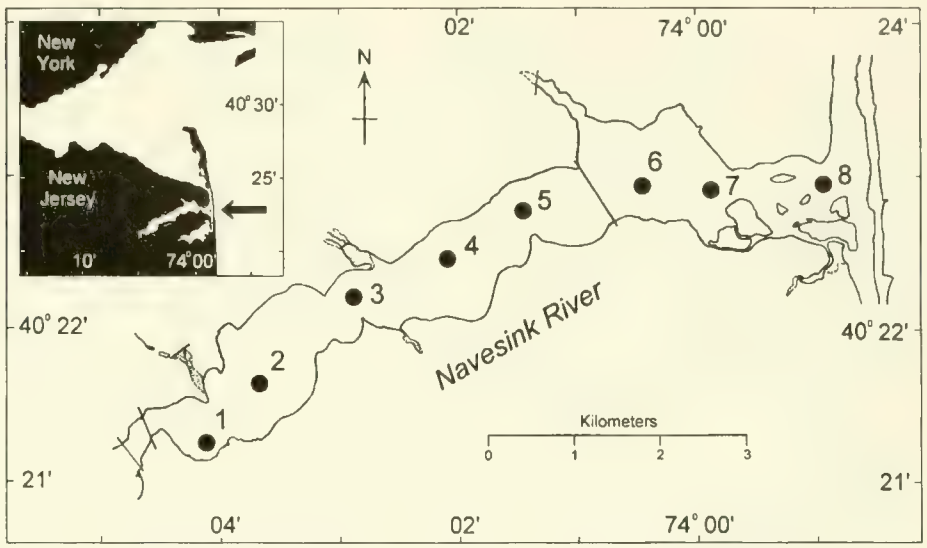

Figure 1

The Navesink River estuary, New Jersey, showing the stations where collections were made for winter flounder during winter and spring 1997.

Field collections

To monitor the location, reproductive condition, and sex ratio of winter flounder in a wild population, weekly daytime otter-trawl surveys were conducted from 7 February to 24 April 1997 in the Navesink River estuary, New Jersey (Fig. 1), which is a known spawning area for the species (Scarlett[1]). Eight fixed stations were established approximately 1 km apart throughout the system. Two 5-min tows (at 4.4 ±0.9 km/h) were made at each station with a 5-m semi-balloon otter trawl with 3.5-cm wings and body and a 6-mm codend liner. Abundance of winter flounder was reported in catch per unit of effort standardized as number of individuals per 100 m of tow distance, which was estimated with a global positioning system (GPS).

Winter flounder collected in the trawl surveys were measured to the nearest millimeter of total length, blotted dry, and weighed to the nearest gram. Gender was determined by inspecting the gonads, and each fish was classified as immature, ripe, or spent. The gonads were weighed to the nearest gram, and gonadosomatic indices (GSI) were calculated according to LeCren (1951) as

$$GSI = 100\ (gonad\ weight/total\ body\ weight).$$

The stomach of each winter flounder was removed, preserved in 10% formalin solution, and later transferred to 70% ethanol. Diet was analyzed as in Stehlik (1993), and fullness of the foregut was estimated visually on a scale from 0% to 100%. Prey items were identified to the lowest possible taxon and the proportion of the total volume of stomach contents con-

[1] Scarlett, P. G. 1991. Temporal and spatial distribution of winter flounder (*Pseudopleuronectes americanus*) spawning in the Navesink and Shrewsbury Rivers, New Jersey. Dep. of Environmental Protection, Div. Fish, Game and Wildlife, Bureau of Marine Fisheries, Nacote Creek Marine Fisheries Laboratory, Star Route, Abseron, New Jersey, 12 p. Unpubl. report.

tributed by each prey type was estimated visually (Williams, 1981). Fullness was averaged for fish grouped by date, gender, and stage of reproductive development. Fish examined were 63–460 mm TL.

Bottom water temperature, salinity, and dissolved oxygen were measured weekly at each station with YSI (Yellow Springs Instruments) oxygen and temperature-conductivity meters. HydroLab DataSonde II instruments were deployed near the bottom on piers extending from the south shore of the Navesink River near stations 1 and 6 to record temperature, salinity, and dissolved oxygen each hour.

Results

Laboratory observations

Behavior Two forms of simple courtship behavior were observed in the research aquarium: "following" and "avoidance." "Following" was defined as oriented locomotion of one or more fish behind another, typically on the sediment surface. A following could be relatively slow or fast (approx. 20–50 cm/sec), continued for 5–20 sec, and sometimes resembled chasing. Turns by the lead fish were followed by the fish behind, and, in most cases, the distance between fish decreased but contact was never made. In all cases where genders of the fish could be determined the lead was female. One or more "followers" were always male. "Avoidance" was characterized by brief contact (<1 s) between a "follower" and the female being followed, then by rapid acceleration and evasive turning by the female. Typically, the female swam 1–2 m off the bottom. In at least 50% of such encounters additional males converged rapidly on the female, eliciting strenuous evasive swimming by the female.

Our observations of spawning in winter flounder were relatively similar to those of Breder (1922), except that females never initiated spawning. Spawning occurred after initial contact by a male as described above. Instead of fleeing, the female remained near the sediment surface (<1.0 m above it) and the pair immediately made several very rapid circles with diameters typically less than two body lengths. Spawning events could be detected even in the far reaches of the tank during darkness because the female nearly always rotated momentarily to the vertical position so that the white underside of her body was clearly visible on the outside of the circles. Participation by multiple males in the spawning event was common, and in approximately 10% of spawning events, one to several males converged on the spawning location immediately after the female had departed, making rapid undulating motions on the sediment surface. Despite convergence of males on spawning females and spawning locations, agonistic behavior among males was never observed. In less than 2% of observed spawning events, a second spawning by the same female occurred a short distance from the first encounter. In most cases the female avoided further contact.

Spawning Spawning began on 8 February 1997, about 2 weeks after the fish were introduced into the research aquarium. One or more spawnings occurred in camera view every day, except 14 February, until 1 April (Fig. 2A); maxima were evident in mid-February and mid-March. The last spawnings were observed on 8 April. In total, 211 spawning events were recorded, 34% of which were definite. In analyses that follow, we considered the "spawning season" in the aquarium to be the period between 8 February and 8 April, 1997. The "postspawning season" was the remainder of the observational period, 9 April through 13 May 1997.

Spawning began near or just before sunset (1700–1800 h) and reached maximum frequency around 2100 h (Fig. 3A). Seventy-five percent of all observed events occurred before midnight. Although some spawning occurred as late as 0430 h, only 10% occurred after 0200 h, when the fish became relatively inactive.

When the total number of spawning events during the observation period was extrapolated to the total dimensions of the aquarium and divided by the ten females in the system, we estimated that the average female flounder spawned 40 times during the reproductive season. It is unknown whether individual fish spawned over this extended observation period. However, given that the mean total number of spawns per night was just six, individuals probably spawned over a period of at least one week. Two facts suggest that a subset of the females may have been completely spent during the first three weeks of the spawning period: the nightly spawning frequency was bimodal, with a minimum on 2 March (Fig. 2A), and female feeding increased rapidly after approximately 3 March (Fig. 4).

None of the observed spawning events involved more than one female flounder, but multiple males were engaged in the majority of spawnings. In 151 events with records for the number of males, only 22.5% were pair spawnings, 11.3% had two males, 3.3% had three males, and the majority involved four to six males (62.9%). Given these numbers, a conservative estimate for the total number of male spawnings within camera view is 780. By extrapolating to total tank dimensions and dividing among the ten males

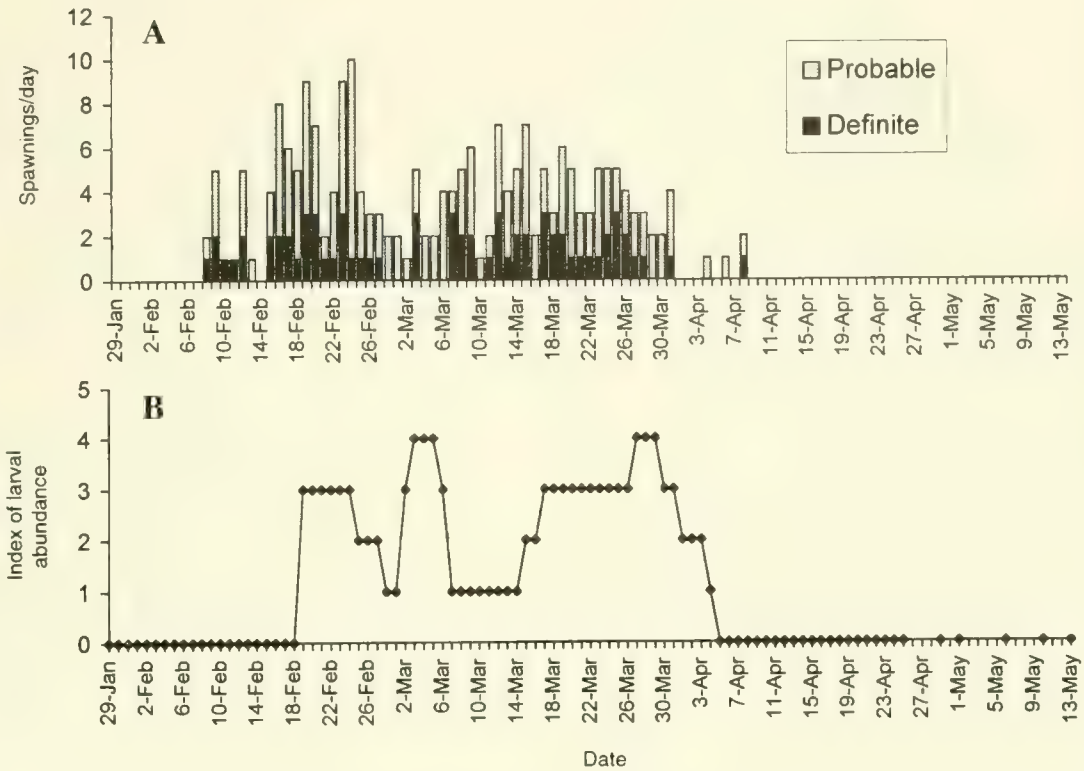

Figure 2

(A) Number of winter flounder spawnings observed on a daily basis in the research aquarium. **(B)** Larval abundance in the research aquarium as a function of date. The index represents only newly hatched larvae because older larvae were extracted by aquarium filtration.

in the system, we estimated that each male (on average) spawned approximately 147 times during the season.

Larval abundance The first winter flounder larvae were observed in the aquarium on 19 February, 11 days after the first spawning was observed. A week of low larval abundance occurred in March, but larvae were constantly present until 5 April (Fig. 2B). Because there was no appreciable food for fish larvae in the aquarium, most of the larvae observed were at yolksac and early stages.

Courtship behavior The spawning season was characterized by a high frequency of following behavior (Fig. 5A). Only a small amount of following was observed in the days before and after the spawning season, but 50–200 following events were observed each night between 8 February and 8 April, decreasing steadily after mid-March. This pattern reflected spawning frequency (Fig. 2A), and there was a weak but positive correlation (r=0.531, P<0.001) between the two forms of behavior.

Avoidance events were approximately one order of magnitude less frequent than following events (Fig. 5), but the seasonal patterns were similar, and there was a positive correlation between these behaviors (r=0.786, P<0.001). The correlation between avoidance and spawning was also positive (r=0.441, P<0.001). Most courtship behavior occurred after sunset between 1700 and 0400 h, with a broad mode around 2100 h (Fig. 3, B and C). Very few interactions occurred in daylight.

Feeding and growth The seasonal pattern of feeding was entirely different from the patterns of spawning, following, and avoidance behaviors. First feeding occurred on 10 February, then increased slowly over time—some apparent oscillations, however, were embedded in the overall trend (Fig. 4). For example, an approximately 10-day periodicity occurred between 12 February and 20 March; this was independent of the dates when fresh food was added. All feeders that could be identified prior to 18 March were female. Females were responsible for 90% of all feeding events recorded (n=3673), and this percentage

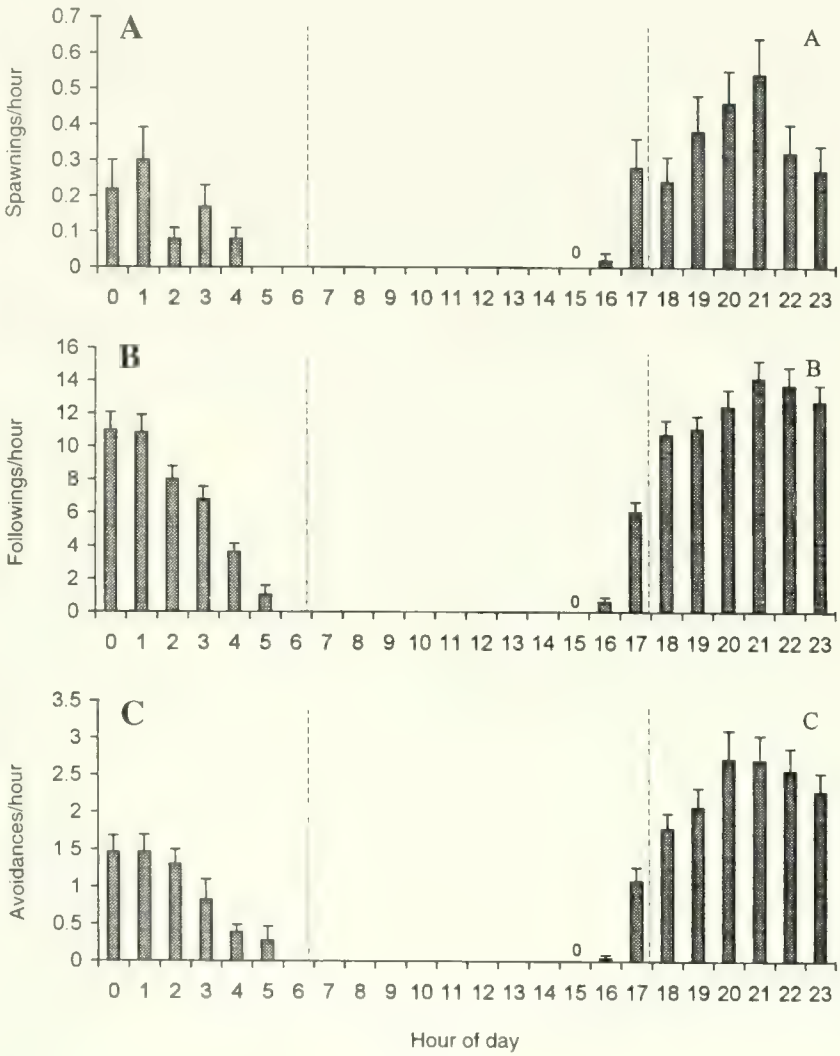

Figure 3

Hourly frequency of **(A)** spawning, **(B)** following, and **(C)** avoidance behavior by winter flounder during the spawning season in the research aquarium. Values represent mean numbers of observed events per hour ±1 standard error. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

did not differ appreciably between spawning (90.3%) and postspawning (89.8%) periods.

It is possible that feeding frequency was related to water temperature. During the time when water temperature was 4°C (until 25 March), average feeding frequency was 14 bouts/day (SD=17, n=45). During the period when temperature was 9°C (26 March–8 April), feeding frequency increased to 94 bouts/day (SD=47, n=11), and when the temperature was 15°C (14 April–13 May) there were 159 bouts/day (SD=107, n=17).

Diurnal feeding periodicity was similar in males and females. During spawning season, most feeding occurred in the hours immediately following sunset and ended before sunrise (Fig. 6, A and C). After spawning ended, feeding (particularly by females) was dispersed throughout day and night, and maximum feeding occurred from afternoon to early evening, primarily 1300–1900 h (Fig. 6B). The least feeding activity occurred from approximately midnight until 1100 h. Feeding by males during the postspawning season continued to be much less frequent than feeding by females; however, the diurnal pattern shifted similarly to an earlier period of maximum activity (Fig. 6D).

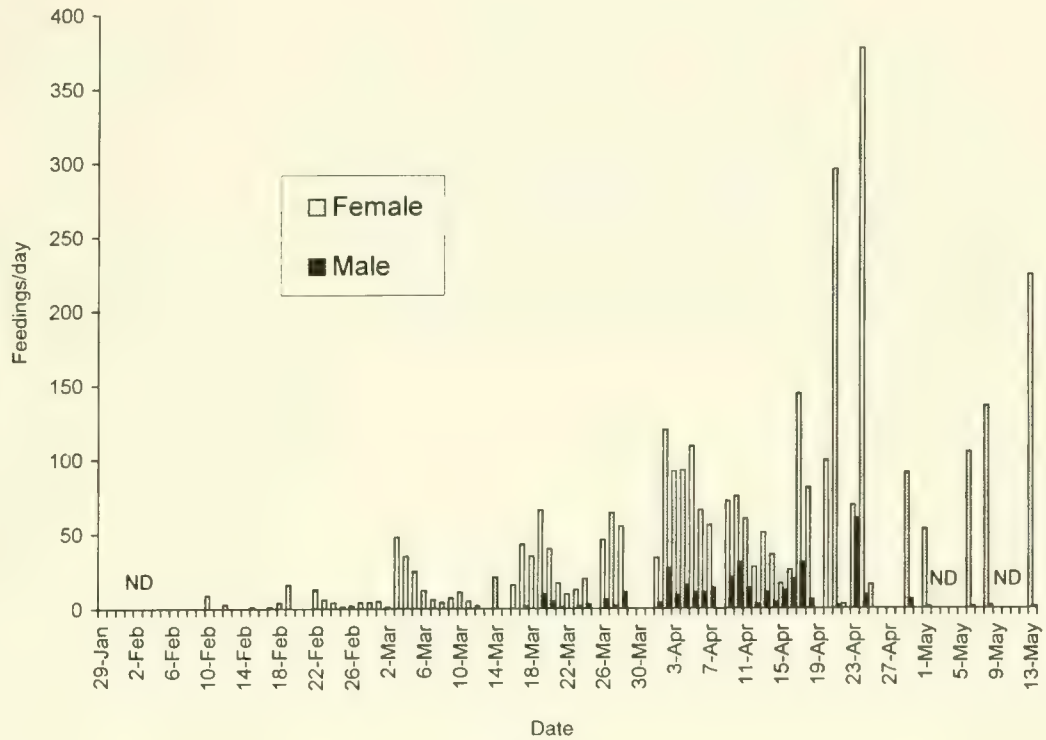

Figure 4

Total number of feeding bouts observed in the research aquarium shown on a daily basis for female and male winter flounder. ND = no data available.

Most female winter flounder demonstrated growth in total length (mean=1.0 cm, SD=1.0) during the three-month experimental period, despite the cold temperature and high spawning activity. Change in length of males (mean=0.1 cm, SD=0.6) was less but the gender difference was not significant (Student's t=–1.91, df=7, P<0.098) because of large individual variation.

Locomotory pattern General activity in winter flounder during the spawning season began near sunset and remained high throughout the night until sunrise (Fig. 7, A and C). After spawning ended, approximately equal levels of activity were observed during day and night, with highest levels during afternoon and evening hours. Diurnal patterns of locomotion were somewhat different in males and females. During the spawning season, male fish began moving somewhat earlier in the evening than females, and the general level of activity was higher. Postspawning, female fish shifted more strongly to an afternoon activity pattern whereas males continued a high level of activity into the night and early morning hours (Fig. 7).

Swimming speeds of winter flounder were generally near 20–25 cm/sec, and there was no apparent effect of date or time of day during active hours. However, male fish were significantly faster (overall mean=26.1 cm/sec, SD=6.6) than females (mean=21.2 cm/sec, SD=4.6; Student's t=14.61, P<0.001).

Field observations

Physical conditions Temperature in the Navesink River estuary ranged from 2.2°C in mid-February to 11°C at the end of the field study in late April, and there was relatively little temperature variation among the eight field stations (Fig. 8A). Salinity near station 6 in the eastern part of the study area ranged from 15 to 23 ppt over the study period. At station 1 in the western part of the study area, salinity was 10–21 ppt, except for a brief period of low salinity (7–10 ppt) on 1 April 1997. Therefore, the entire sampling area was polyhaline, and there was a slightly wider range of salinity in the west than in the east. Dissolved oxygen was always high (>8 mg/L) at the two sites where measurements were made continuously.

Population structure, reproduction, and migration Numbers of winter flounder in the Navesink River

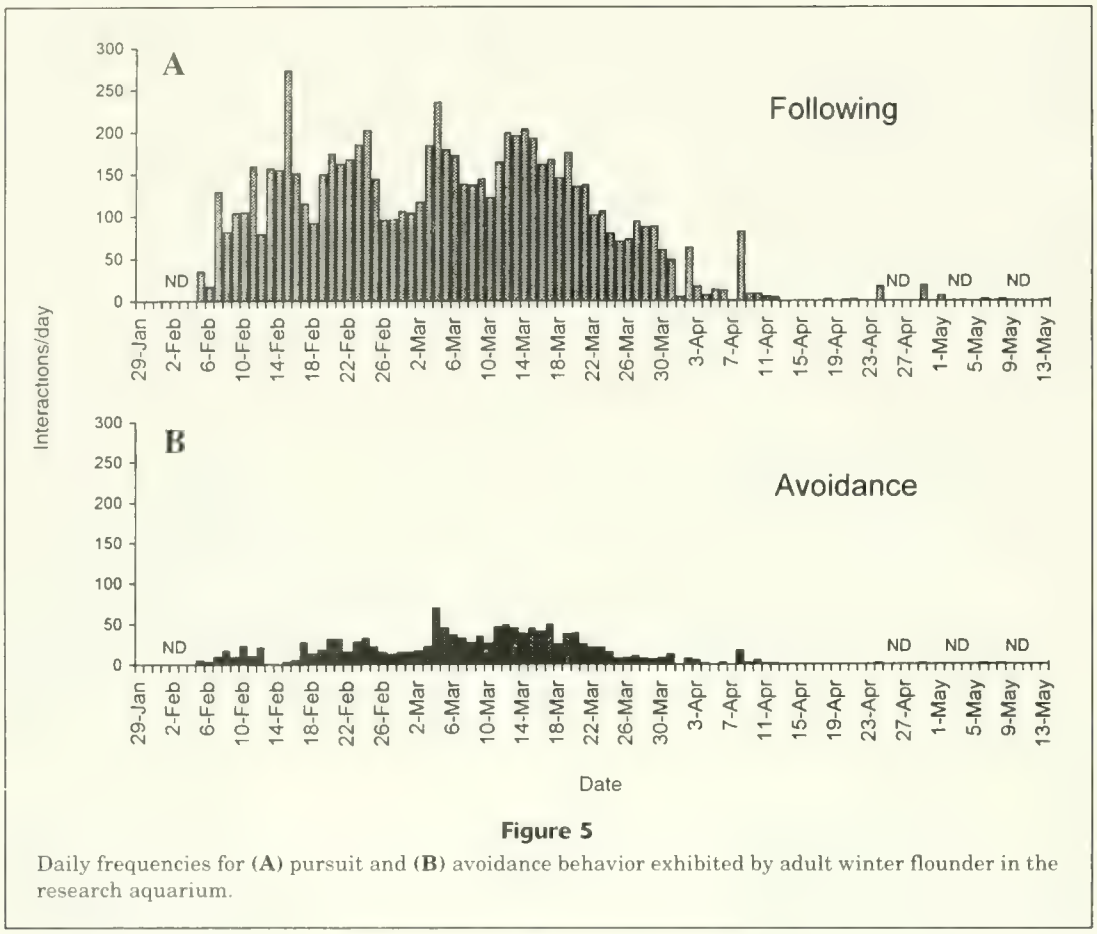

Figure 5

Daily frequencies for **(A)** pursuit and **(B)** avoidance behavior exhibited by adult winter flounder in the research aquarium.

estuary increased steadily between mid-February and early March, concurrent with the rise in water temperature (Fig. 8). Abundance remained relatively stable for the remainder of the collection period. Of the 389 winter flounder collected, 49% were female (mean length=28.9 cm, SD=8.9) and 32.5% were male (mean=25.1 cm, SD=6.9). Gender could not be determined for 18.5%, all of which were small individuals considered to be age-1 fish (mean=10.2 cm, SD=2.3). Females were significantly more abundant than males (Table 1; F=4.62, P<0.05), with a sex ratio of 1.5 to 1, and this pattern was consistent throughout the sampling period; analysis of variance (ANOVA) showed a nonsignificant *Date × Gender interaction* (P=0.58; Table 1).

The majority of ripe female flounder were collected in the first half of the survey period (Fig. 9A); all of these fish were larger than 20 cm TL. Ripe females were divided into two obvious groups based on gonadosomatic index (GSI). Sixty-five percent of ripe females had GSIs greater than 20% (mean=30.9, SD=9.1). A second group of nearly spent females had GSIs of 3–8%. All female winter flounder collected after mid-March had GSIs less than 6%.

Table 1

Results of analysis of variance on catch data for winter flounder in the Navesink River during winter 1997. ANOVA was performed on natural log-transformed data on catch per unit effort. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = $P > 0.05$.

Source of variation	df	Sum of squares	F ratio
Date	9	0.002	3.27 **
Station	7	0.004	7.25 ***
Gender	1	0.0003	4.62 *
Date × Station	63	0.009	2.10 ***
Date × Gender	9	0.0005	0.84 ns
Station × Gender	7	0.004	7.22 ***
Date × Station × Gender	63	0.003	0.59 ns
Error	160	0.011	

Male winter flounder formed two size groups, small fish (<20 cm TL) assumed to be age-1 fish and larger individuals (20–35 cm TL). Through the end of February all males larger than 20 cm were reproduc-

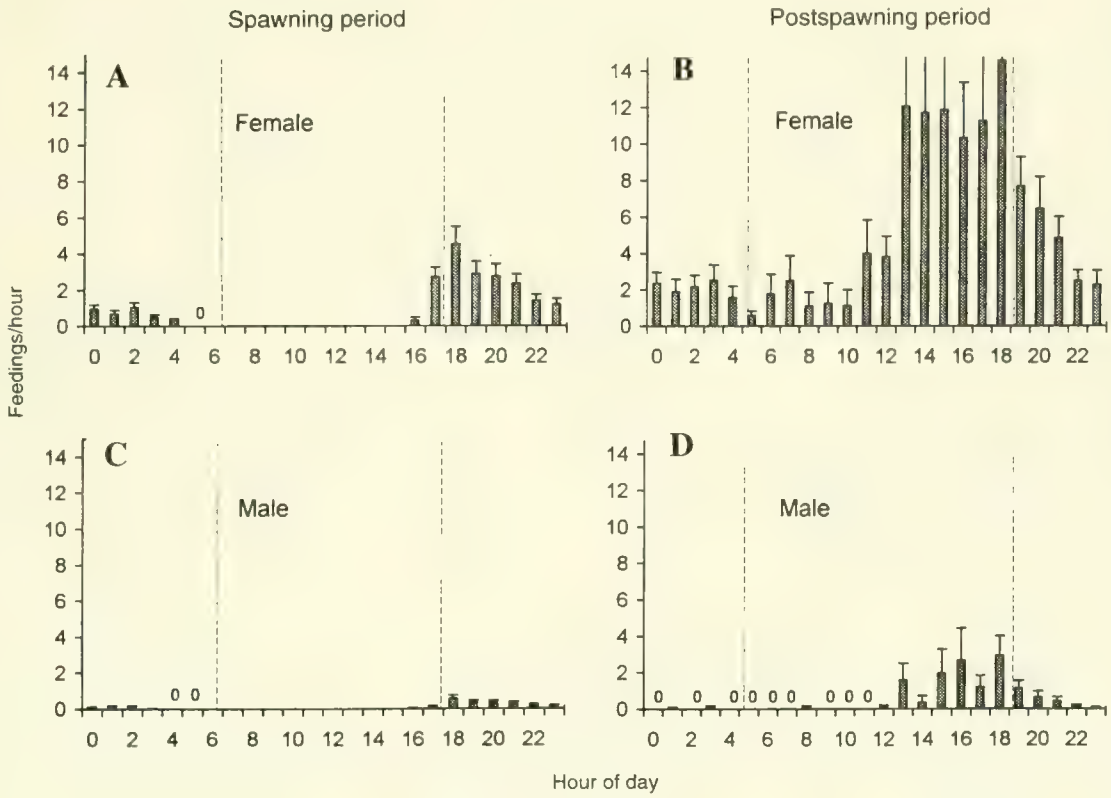

Figure 6

Hourly frequency of feeding during spawning and postspawning periods for **(A, B)** female and **(C, D)** male winter flounder in the research aquarium. Values represent mean numbers of observed events per hour ±1 standard error. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

tively ripe, as were 40% of males between 10 and 15 cm. A steady decline in male GSI began in March (Fig. 9B), but ripe males (mean GSI=7.3, SD=4.4) were collected later than ripe females, through 11 April.

Although the number of fish collected at any one station was not large, the *Station × Gender interaction* in the ANOVA indicated that male and female flounder had different distributional patterns in the estuary (Table 1). Males were more abundant than females at stations in the lower estuary (stations 7 and 8), whereas females were more abundant in the middle and upper reaches (stations 1–6) (Fig. 10). These gender-specific distribution patterns were generally consistent, as indicated by the nonsignificant *Date × Station × Gender* interaction term in the ANOVA (Table 1). Ripe males were collected throughout the estuary in proportions ranging from 14% of individuals at station 6, to 100% at stations 1 and 2. In contrast, all ripe females were collected at stations 1–4, with the exception of one partially spent female collected at station 7.

The length distribution of female winter flounder at most of the sampling stations showed two modes (Fig. 11). Large females (mean length=29.7 cm, SD=0.6) were collected at all eight stations but were most abundant in the middle reach (stations 3–6). Small females (<20 cm TL), all of which were reproductively immature, were most abundant in the upper estuary, with approximately equal numbers of small fish at stations 1–4. Size groups were less obvious in male winter flounder (Fig. 11), but it is clear that the mean size of male fish was larger at stations in the lower river (stations 5–8) than in the upper river, and small fish were most abundant at stations 1–3. From 28 March through the end of the sampling period, large numbers of flounders were collected only at station 6. Virtually all the fish in the lower river during this late part of the collecting season were spent.

Feeding Stomach fullness in winter flounder varied with date, gender, and age (Fig. 12). Highest full-

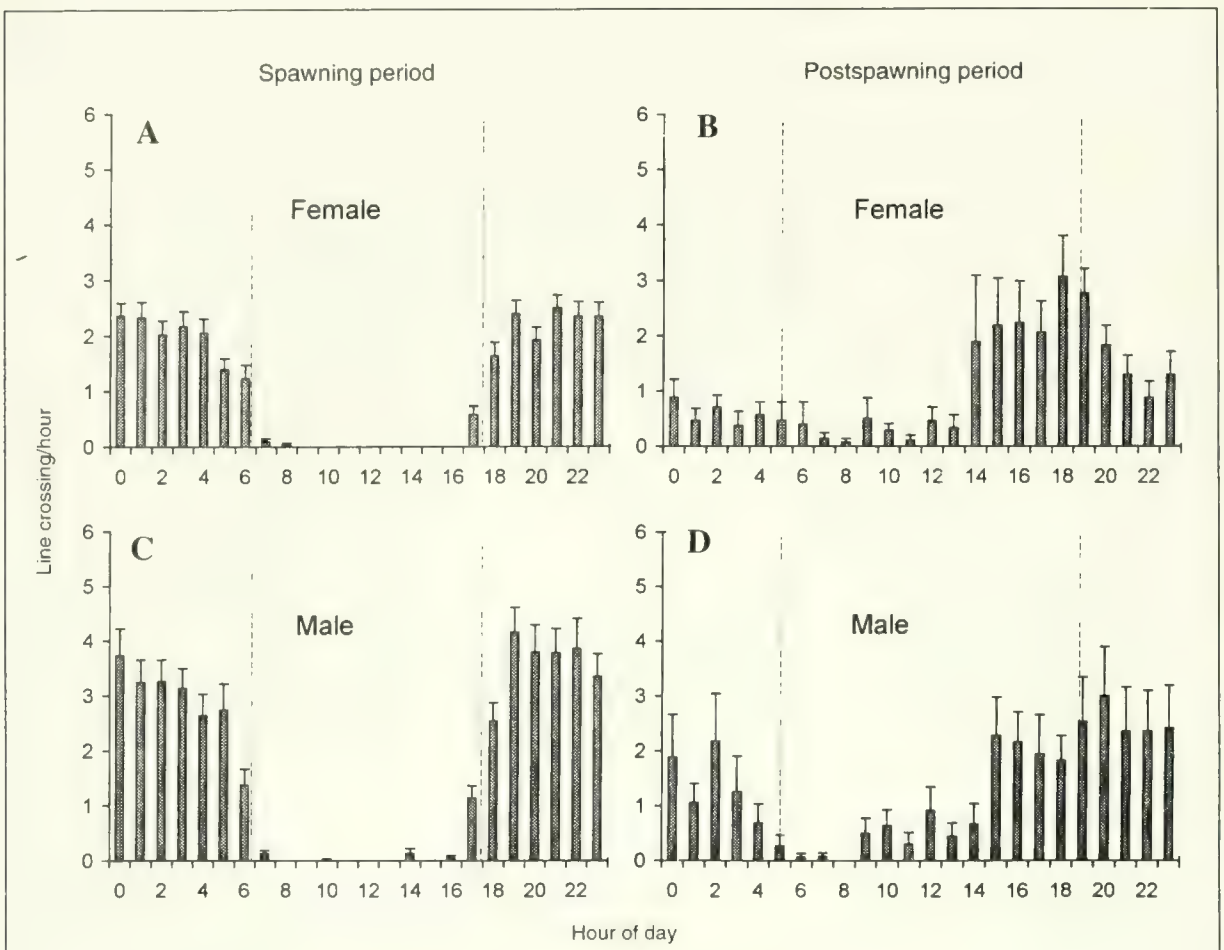

Figure 7

Locomotory activity in adult winter flounder in the research aquarium shown on an hourly basis for **(A, B)** females and **(C, D)** males during the spawning and postspawning periods. See text for the method used in generating this index of activity. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

ness indices (59%–84%) occurred in immature fish, most containing substantial amounts of food. Average fullness in females was also high throughout the survey period (60%–80%), but variation was large and associated with reproductive state. Ripe females had an average fullness of just 24%, whereas spent females had an average fullness of 72%. Variation among males was even higher, with an obvious increase in fullness from about 1% early in the survey to a range of 70%–90% during the last three collection dates (Fig. 12). Ripe males had average stomach fullness of only 17%, whereas average fullness of spent males was 69%. Therefore, the rapid increase in stomach fullness of males in late March was associated with rapidly declining numbers of ripe males. Stomach fullness was weakly correlated with GSI in both females (r=–0.439) and males (r=–0.582) because fullness in fish with a low GSI spanned the entire range from 0%–100%.

Siphons of soft clam (*Mya arenaria*) were the most abundant prey items taken by winter flounder, on the basis of both percentage volume and frequency of occurrence. Of the 257 flounders that contained prey, 150 contained siphons with diameters of 3–13 mm. However, diet varied with collection site (Fig. 13). Siphons of *M. arenaria* were most abundant in fish collected in the middle reach of the estuary (stations 3–6), whereas another clam, *Macoma balthica*, was most abundant in fish from the upper reach (station 1). Ampeliscid amphipods, mysids, shrimps, and other crustaceans were the most important food items in the lower estuary.

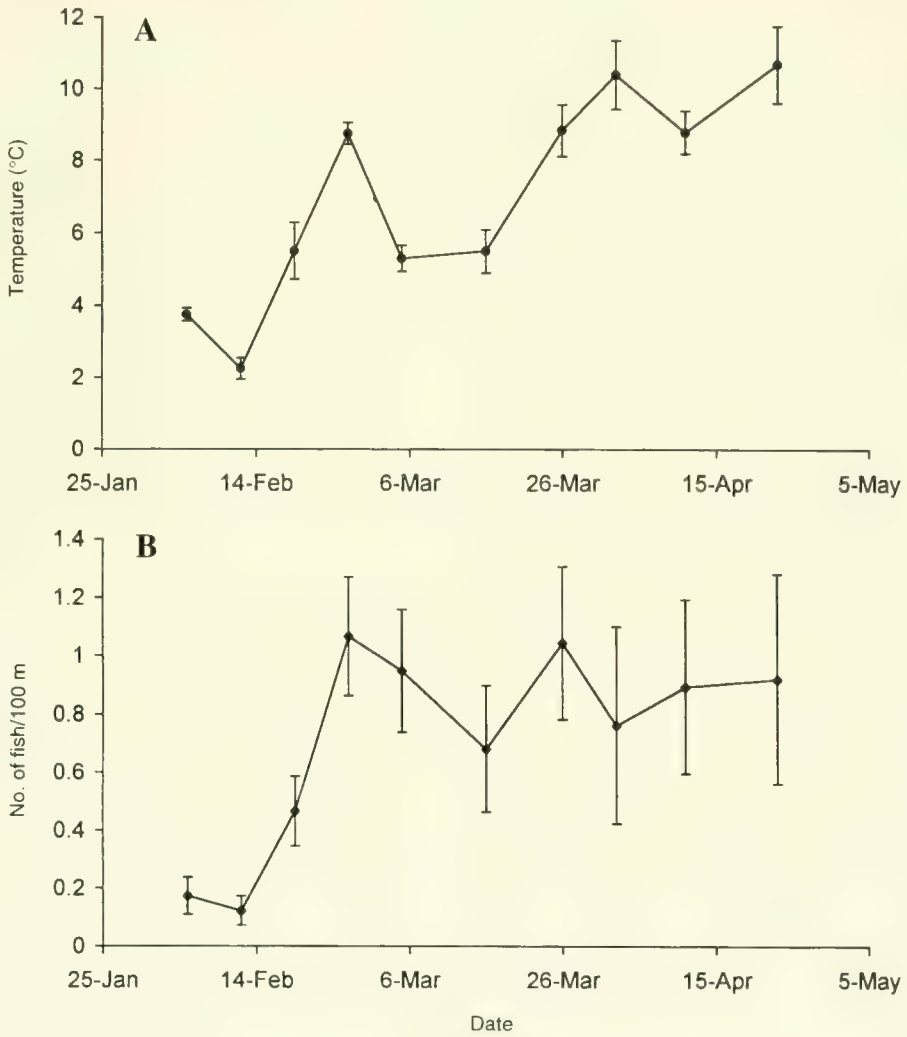

Figure 8

(A) Water temperature and **(B)** abundance of winter flounder in the Navesink River estuary during winter and spring 1997. Temperature values are means and ranges of temperature at the eight sampling stations. Values for flounder abundance are mean catch (±1 standard error) per 100-m distance over the bottom sampled by a 5-m otter trawl.

Discussion

Spawning behavior

Direct observation of spawning behavior has been documented for only a few flatfish, but spawning modes appear to vary substantially among species. Midwater pair-spawning has been observed in plaice (*P. platessus*; Forster, 1953), and in Dover sole (*Microstomus pacificus*; Baynes et al., 1994), but winter flounder spawned near the bottom and pairwise spawning (22%) was less common than spawnings involving multiple males (78%). Also, winter flounder spawning may be less elaborate or ritualized than in plaice or Dover sole or Caribbean bothids (Konstantinou and Shen, 1995). Although this could be an artifact of confinement, our research aquarium, with a bottom surface area of 46 m^2 and 3 m depth, was much larger than tanks where pair spawning has been observed in other species and where the density and size of fish were lower.

Our long-term observation of a single spawning population in the aquarium allowed us to record several different forms of reproductive behavior not reported earlier (Breder, 1922). Most notably, we were able to observe and record individual encounters

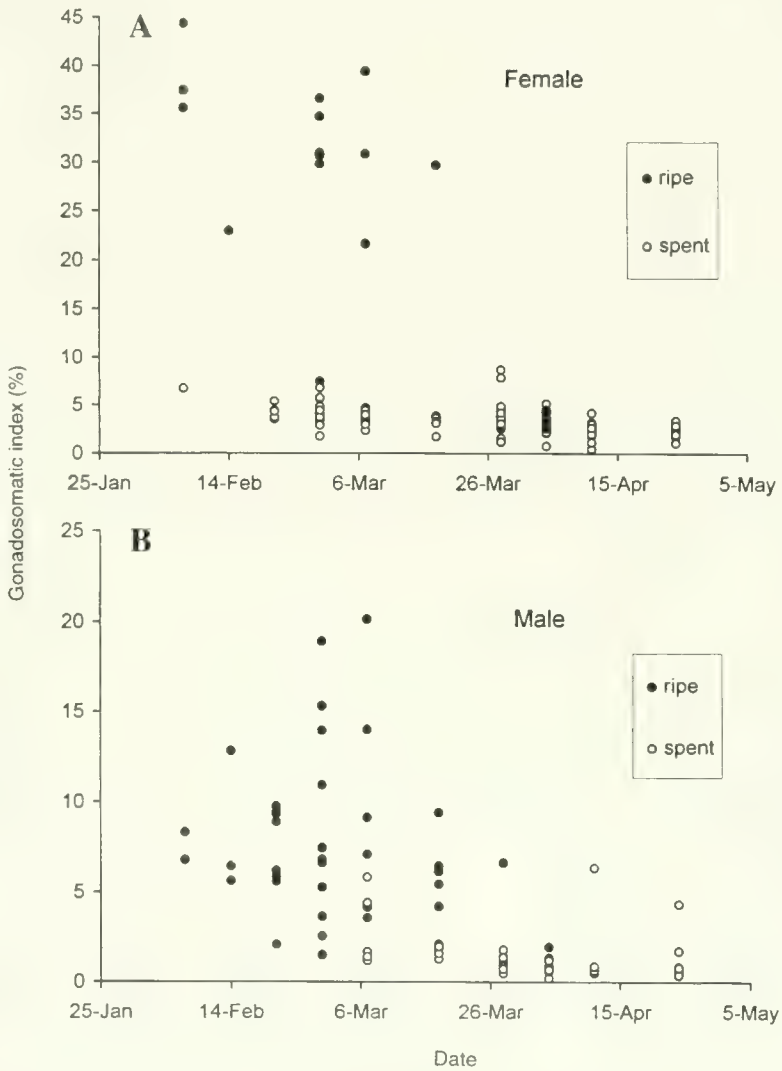

Figure 9

Gonadosomatic index (GSI) for winter flounder **(A)** females and **(B)** males shown as a function of collection date. The index was calculated according to LeCren (1951) as $GSI = 100(gonad\ weight/total\ body\ weight)$. Observational conclusions about the reproductive state of individual fish are shown by dots for ripe fish and circles for spent fish. Note the different *y*-axes.

between males and females. Unlike Breder, and in thousands of observed encounters, we never observed females initiating spawning activities. Breder acknowledged that his relatively small tanks may have altered normal behavioral patterns and was correct in predicting that males would be more active than females in a more open environment. In fact, males attempted to initiate spawning in the laboratory long before and after females were receptive. A similar phenomenon most likely occurs in the field, where males are ripe and capable of spawning for a longer period of time than females. Similarly, Rijnsdorp (1989) has observed that male plaice are in spawning condition for a period twice as long as that for females. As in our observations with winter flounder, Baynes et al. (1994) observed that males of *Microstomus* were much more active than females, and male attempts to initiate spawning were often rejected.

Male winter flounder were able to detect the presence of a spawning female from distances of at least 5–10 m in the research aquarium and frequently con-

verged suddenly on a spawning pair or group. A variety of sensory mechanisms could play a role in detecting opportunities for egg fertilization. Male fish may respond to the obvious visual signal of light reflected from the white underside of spawning fish. It is also possible that hydroacoustic cues were emitted from vigorous bouts of spawning that occurred just above the bottom. It is less likely that spawning was detected by an olfactory cue because there was almost instantaneous response to spawning activity and there was little horizontal current in the aquarium. However, olfactory cues may be important in certain circumstances. Occasionally, males converged on locations where spawning had occurred although the spawners had departed, and these spawning locations were sometimes visited by additional males for several minutes after the initial spawning event. Future research will be needed to determine the precise mechanisms of spawning group formation and detection.

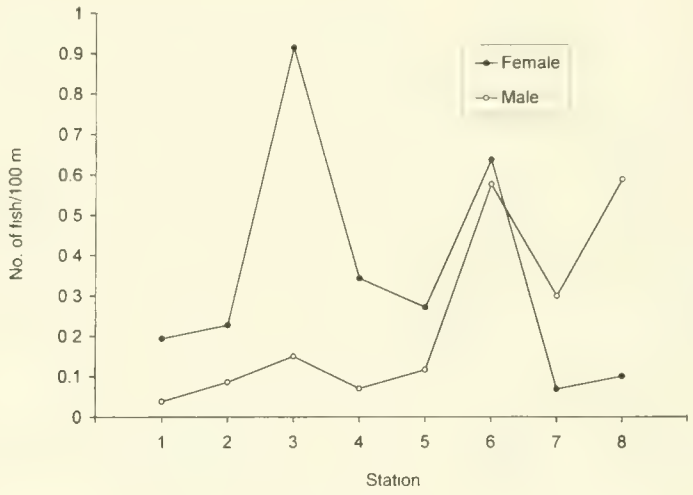

Figure 10

Mean catch by station number of male and female winter flounder per 100 m distance over the bottom in the Navesink River estuary. Values plotted are means for all dates combined.

In female winter flounder just one batch of oocytes matures per year (Burton and Idler, 1984); nevertheless, spawning in the aquarium population of winter flounder had a duration of 60 days. It is clear that individual females spawn many times over a period of at least one week, and perhaps longer. Circumstantial evidence indicates that individual males were capable of spawning over most of the reproductive season in the research aquarium. Large numbers of males were often engaged in single spawning events; the total number of spawnings yielded a high average spawning frequency by males that would necessitate several weeks of spawning by each; and feeding by males did not begin until most females stopped spawning. It is unknown whether male winter flounder produce more than one batch of sperm or simply release one batch over time (Bert et al., 1988).

Spawning in the aquarium occurred over a broad range of times, but always during hours of darkness or just before. Nocturnal spawning in winter flounder is probably a function of endogenous diurnal rhythms rather than light level because Breder (1922) noted that spawning occurred between 2200 and 0330 h even under artificial light. Spawning times vary with flatfish species and are probably species-specific. For example, plaice (Nichols, 1989) and other pleuronectids (Woodhead, 1966) are also known to spawn primarily at night, but *Bothus ocellatus* spawns only around the time of sunset (Konstantinou and Shen, 1995).

The role of multiple releases of eggs and sperm is poorly understood but may be important in the reproductive biology and recruitment of winter flounder. Although release of gametes could not be recorded or verified beyond the fact that larvae were produced in the aquarium, it is evident that numerous males spawned in response to one female. It is likely, therefore, that eggs released in a single spawning event were often fertilized by more than one male. Given that the average female fish spawned 40 times during the reproductive season in the aquarium and that most of the males appeared to remain ripe throughout the observation period, it is likely that many, if not all, of the males could have contributed genetic material to the offspring of each female. Genetic diversity of embryos produced in the field could be high for similar reasons.

Although male winter flounder appeared to be in a constant state of readiness for spawning, future experiments will be needed to determine whether frequency of spawning and fertilization success is uniform among individuals and how this might be influenced by size structure, sex ratio, or density of fish on the spawning ground. For example, small (10–15 cm) but reproductively ripe males were abundant in the Navesink River estuary. It is possible that these small individuals have a lower frequency of success than large males in inducing females to spawn, given the order-of-magnitude difference in body weight between 10 and 22 cm fish. However, Baynes et al. (1994) observed female Dover sole spawning with males smaller than themselves, and

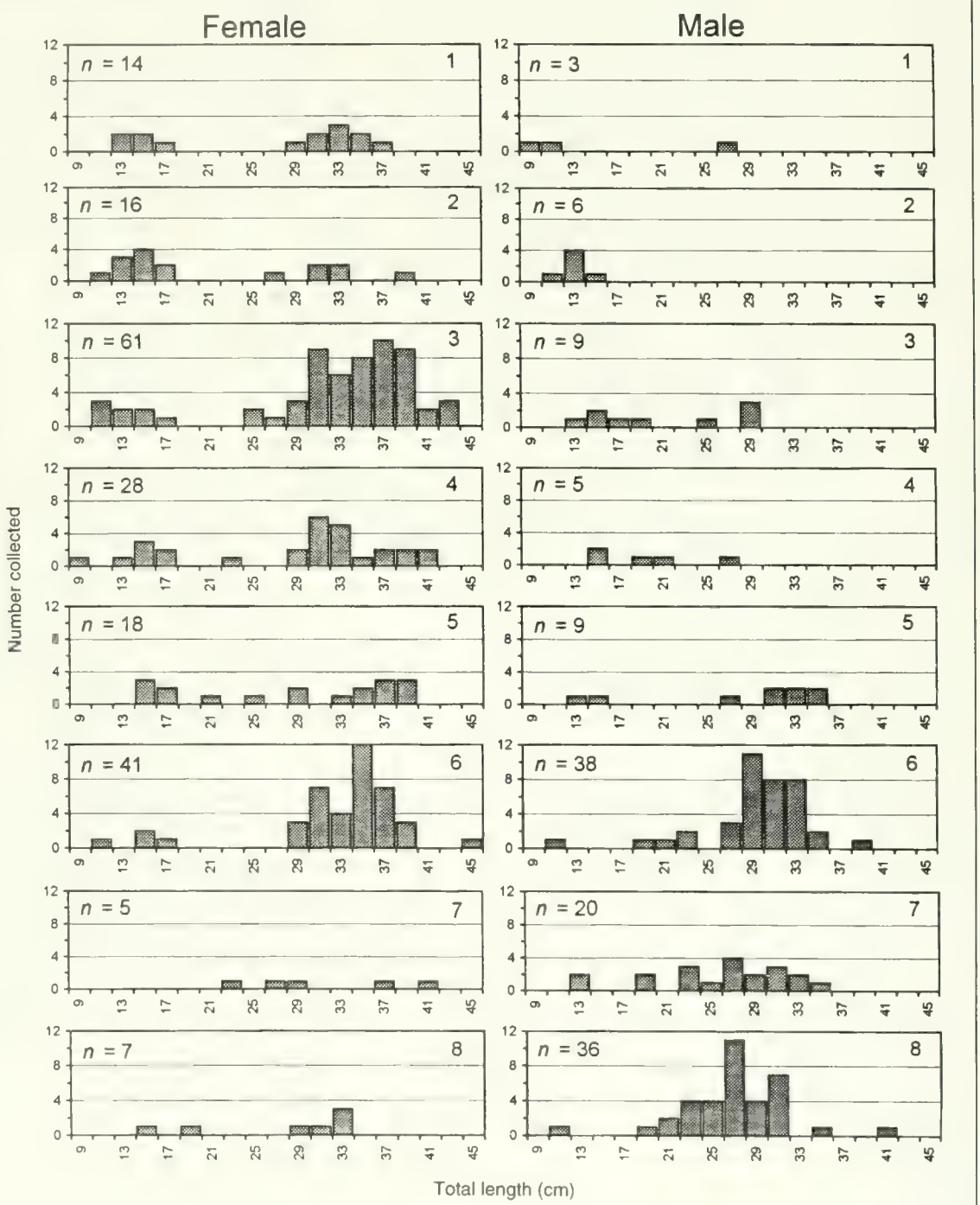

Figure 11

Length-frequency distributions for female and male winter flounder in the Navesink River estuary, plotted by field station.

the same may occur with winter flounder. On the other hand, most fertilization by small males may occur during group spawning. "Sneaking," whereby subordinate males approach and fertilize some of the eggs when a pair is spawning, is a reproductive behavior common in a variety of fishes (Chan and Ribbink, 1990; Oliviera and Almada, 1998). We observed no overt agonistic behavior in our long-term experiment, and there is no reason to believe that small males do not contribute to the reproductive population.

Spawning, migration, and habitat use

Previous studies have shown that winter flounder in the mid-Atlantic region migrate to shallow inshore waters to spawn during the late winter (Perlmutter, 1947; Poole, 1966; Scarlett and Allen, 1992), and it is known that the Navesink-Shrewsbury River estuarine system is an important spawning ground (Phelan, 1992; Scarlett[1]). Phelan's study and our investigation provide direct evidence that winter flounder immigrate to the Navesink estuary between early February and March. Flounder abundance was lowest when water temperature was lowest (2.2°C in mid-February) and increased rapidly with subsequent temperature rise. In fact, high and relatively constant catches of winter flounder occurred in the Navesink estuary at temperatures of 6–11°C. This is consistent with earlier observations that adult winter flounder emigrated from bays in southern New Jersey when water temperature declined below 3.5°C and returned when temperature rose to 6°C (Danila, 1978). Most adult males and females had ripe gonads upon entry to the system in late winter, and most were spent by the end of April. This pattern of seasonality is consistent with previous findings (Pearcy, 1962; Scarlett and Allen, 1992).

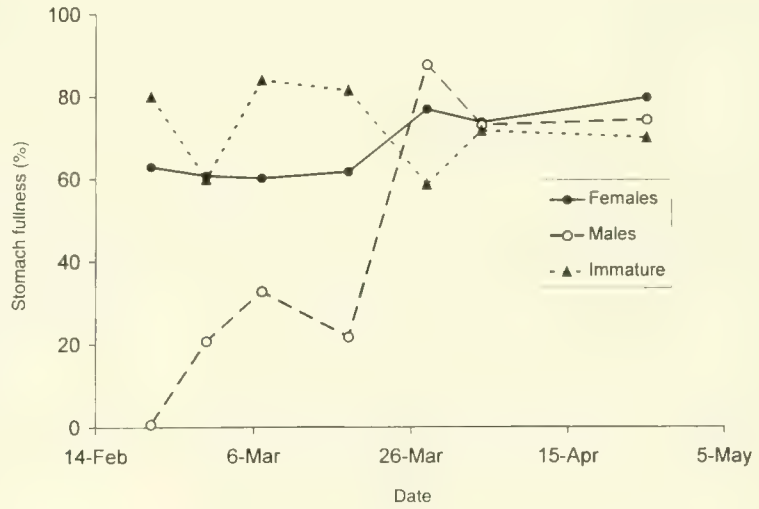

Figure 12

Temporal variation in percent stomach fullness of winter flounder in the Navesink River estuary. Fullness indices are shown by adult gender and for immature fish.

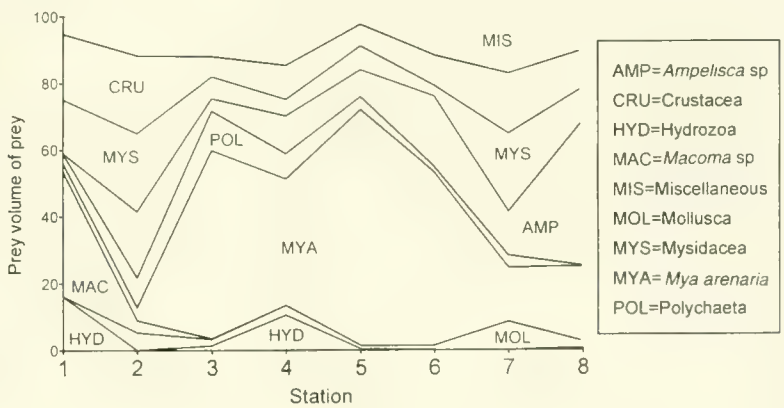

Figure 13

Composition of diet by percentage volume in winter flounder collected at eight stations along the length of the Navesink River estuary during winter and spring 1997.

It is likely that the most important spawning area for winter flounder in the Navesink River was in the middle reach. Reproductively ripe male winter flounder were found throughout the estuary; however, highest numbers of ripe females were found west of station 5, and only one nearly spent female was collected farther down the estuary. Scarlett and Allen (1992) found that the middle reach of the Manasquan River estuary, New Jersey, was a major spawning ground for winter flounder, as were the upper reaches of the Mystic River estuary, Connecticut (Pearcy, 1962), and Narragansett Bay, Rhode Island (Powell[2]).

Several different physical and chemical factors could affect the location of spawning habitats. Temperature may have influenced the seasonal migration to the Navesink estuary; however, there was little variation in temperature along the axis of the estuary, and other factors probably influenced exact spawning location. McCracken (1963) found that adult winter flounder died in 8 ppt salinity; therefore, upstream migration is probably limited by this variable. Neither males nor females were abundant in locations where salinity was frequently near or below 10 ppt.

[2] Powell, J. C. 1989. Winter flounder tagging study, 1986–1988, with comments on movements. Rhode Island Division of Fish, Wildlife, and Estuarine Research, P.O. Box 218, West Kingston, Rhode Island 02892. Unpubl. report.

The location of spawning in an estuary may also be related to temperature and salinity requirements of the demersal eggs. Scarlett and Allen (1992) collected eggs at salinities of 14–32 ppt and temperatures of 0.9–10°C in the Manasquan estuary, about 30 km south of our study site. Rogers (1976) found that the highest proportion of viable hatches occurred at 3°C over a salinity range of 15–35 ppt. At temperatures over 3°C, the optimal range was 15–25 ppt, which closely matches temperature and salinity ranges in the middle reach of the Navesink River.

Other factors that may influence the choice of spawning habitat by winter flounder are hydrodynamic properties and associated sediment characteristics. Strong flood tidal currents that characterize the lower Navesink River attenuate rapidly in the middle reach (Chant[3]). This attenuation is associated with deepening of the estuary and general reduction of sand bars, decrease in the mean grain size of sediments, and increase in sediment organic content (Stoner, unpubl. data). It is unknown whether spawning winter flounder respond to any of these habitat characteristics; however, the depositional qualities of the upper estuary and flood-dominated circulation may aid in the retention of winter flounder eggs and the evolution of habitat choice in spawners. Crawford and Carey (1985) noted that winter flounder spawned in two sites in an estuarine lagoon in Rhode Island where hydrodynamic features retained larvae. It is plausible that habitat choice, cued by either fine-grained sediments or low current velocities, could be associated with such retention features.

Seasonal variation in feeding activity

The general conclusion has been that winter flounder are opportunistic feeders, consuming polychaetes, small crustaceans, molluscs, and other prey according to their abundance (Pearcy, 1962; Richards, 1963; Klein-MacPhee, 1978; Franz and Tancredi, 1992; Martell and McClelland, 1994; Steimle et al., 1994; Carlson et al., 1997). Winter flounder collected in the Navesink River during this investigation consumed a mixture of invertebrate prey, but the vast majority of the diet was siphons of the soft clam *Mya arenaria*. The abundance of spent and feeding flounder in the lower estuary may, in fact, be associated with the observed abundance of this preferred prey in that location.

Cessation of feeding by adult winter flounder during the winter has been noted previously (Tyler, 1972; Martell and McClelland, 1994), but we found that feeding was influenced strongly by gender and reproductive state. Both in the field and in the aquarium, female flounder appeared to resume feeding immediately after they completed spawning for the season. Early feeding probably provides an advantage for female fish because ovarian development for the next spawning season begins immediately after spawning (Burton and Idler, 1984). In the field, males did not begin feeding until the end of March, and feeding in the aquarium was light until after the last spawning events. We conclude that male behavior is dedicated to fertilizing the maximum number of eggs, at the expense of feeding and late winter growth.

There is now substantial evidence for seasonal variation in daily activity and feeding rhythms in winter flounder. During the summer, winter flounder are primarily diurnal in general activity (Olla et al., 1969) and feeding (MacDonald and Waiwood, 1987). Bharadwaj (1988) found that adults fed throughout the day and night in November, speculating that this was related to maturation of gonads for the winter spawning season. In our aquarium observations, adult winter flounder were almost entirely nocturnal throughout the spawning season, remaining buried during the day. Daytime activity began again when spawning was completed and increased throughout the remainder of the postspawning period. Primarily daytime activity during the nonspawning season could be associated with visual predation modes (Olla et al., 1969), but it remains to be determined how mates are located in darkness and why spawning occurs at night.

Conclusions

This study provides the first detailed observations on winter flounder spawning since Breder's (1922) original description over 75 years ago, and the combination of laboratory and field work provides new insight into the biology and ecology of spawners. The behavior of male winter flounder appears adapted to maximize encounters with reproductive females and numbers of eggs fertilized. From our field collections, it is apparent that one-year-old male winter flounder (10 cm TL) are capable of spawning, whereas female spawners all appeared to be at least two years old. Males also became reproductively ripe earlier in the season than did females and remained ripe to a later date than most females. Males were more active than females, had higher swimming speeds, and initiated all spawning events. The males fed very little during the reproductive season and appeared

[3] Chant, R. J. 1998. Institute of Marine and Coastal Sciences, Rutgers University, P.O. Box 231, New Brunswick, New Jersey 08903. Unpubl. data.

to sacrifice winter growth to maintain a high level of reproductive behavior.

Spawning frequency was high in both males and females. Individual females were capable of spawning as many as 40 times over a period of at least one week, and males spawned throughout the season (at a rate at least three times the female rate) and perhaps several times per day. Clearly, individual records of spawning behavior would be useful in understanding the reproductive role of one-year-old males and in determining the duration of spawning in individual females. Given the frequency of spawning in both male and female winter flounder and the fact that several males may release sperm in response to egg-laying by one female, we conclude that the genetic diversity of offspring produced by a female in one year is probably very high.

Although our data provide new insights into the natural history and reproductive behavior of winter flounder, several questions important to sound management of spawning stocks remain to be answered. For example, we do not know if reproductive populations are scattered in estuarine and coastal waters or are concentrated in spawning aggregations on specific spawning grounds. We saw a concentration of ripe fish in the middle reach of the Navesink River estuary, but ripe fish were also present in a variety of habitats in adjacent Raritan Bay during the winters of 1997 and 1998 (Stoner and coauthors, personal obs.), and it is possible that winter flounder spawn in more than one location over the spawning season. It is also important to learn whether or not spawning behavior and reproductive output from a spawning ground are density-dependent.

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Population size of humpback whale, *Megaptera novaeangliae*, in waters off the Pacific coast of Mexico

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Abstract.—The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species whose stocks were drastically decreased by commercial whaling practices prior to 1967. The North Pacific population was estimated to be between 15,000 and 20,000 animals before the practice of whaling. At the time of the commencement of its international protection in 1967, this population may have been reduced to fewer than 1000 individuals. The Pacific coast of Mexico and the Revillagigedo Archipelago constitute one of the main breeding and calving areas for North Pacific humpback whales. The objective of this paper is to present an estimation of abundance of humpback whales in this region based on photographic identification of individual animals. Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. The best estimates of population size for the Mexican stocks were those provided by the modified Jolly-Seber method: 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

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Humpback whales, *Megaptera novaeangliae*, make seasonal migrations between low-latitude wintering areas used for mating and calving and high-latitude feeding areas. The general distribution of feeding areas in the North Pacific covers coastal waters in the western North Pacific from northern Japan throughout the Bering Sea and in the eastern North Pacific as far south as southern California. During the winter breeding season, these whales congregate in three geographically isolated tropical areas: the Ryukyuan, Bonin, and Mariana Islands south of Japan; the islands of the Hawaiian Archipelago; and the Pacific coast of Mexico and the Revillagigedo Archipelago (Rice, 1974; Johnson and Wolman, 1984).

Humpback whales have been listed as endangered since severe reduction of all stocks worldwide by commercial exploitation (Rice, 1974; Gambel, 1976). The number of these whales were estimated to be between 15,000 and 20,000 animals before whaling depleted them during the first half of the 20th century; at the time of its international protection in 1967 this population may have been reduced to fewer than 1000 individuals (Rice, 1974, 1978). However, the reliability of these figures is unknown.

The extent of the recovery in the North Pacific population over the last 25 years is debatable. Estimates of abundance with mark and recapture techniques based upon photo-identification data have been made for different areas of this ocean, but there has been much debate regarding the reliability of such estimates (Darling et al., 1983; Baker et al., 1986; Darling and Morowitz, 1986; Baker and Herman, 1987; Alvarez et al., 1990; Calambokidis et al., 1990; Cerchio, 1998; Calambokidis et al.[1]). There is currently insufficient evidence to assess whether a significant change in abundance has occurred since whaling ceased.

Three main wintering aggregations of humpback whales are recognized off the Pacific coast of Mexico: the Baja California Peninsula; the mainland coast of Mexico (including, Isabel Island, Tres Marias Islands, and the mainland coast); and the Revillagigedo Archipelago (including Socorro, San Benedicto, Roca Partida, and Clarion Islands) (Rice, 1979; Urbán y Aguayo, 1987).

The comparison of photo-identified humpback whales in these wintering grounds showed that there was a greater affinity between whales off Baja California and those off the mainland coast of Mexico than those off either Baja California or the mainland coast and those off the Revillagigedo Archipelago (Urbán et al., 1989; Ladrón de Guevara et al., 1993; Jaramillo, 1995) (Table 1). From these results, two different population units of humpback whales during winter in Mexican waters were previously proposed: the coastal Stock (including Baja California and mainland coast of Mexico), and the Revillagigedo stock (Alvarez et al., 1990; Urbán et al.[2]) (Fig. 1).

Table 1

Matches (above the diagonal) and interchange index[1] (below the diagonal) among the three main wintering aggregations in the Mexican Pacific. Sample size in parentheses.

	Baja California Peninsula (471)	Mainland coast of Mexico (383)	Revillagigedo Archipelago (450)
Baja California Peninsula	—	64	20
Mainland coast of Mexico	0.38	—	23
Revillagigedo Archipelago	0.12	0.18	—

[1] Index of interchange.
This index quantify the degree of interchange among two samples (among regions) that accounted for sample size:

$$Index\ of\ interchange = (m_{12} / (n_1 \cdot n_2)) \cdot 1000,$$

where n_1 = whales identified (captured) in sample 1;
n_2 = whales identified in sample 2; and
m_2 = captured whales from sample 1 recaptured in sample 2.

(see Baker et al. 1985; Cerchio et al., 1998)

This division of winter aggregations is also supported by mitochondrial DNA lineage analyses (Medrano-Gonzalez et al., 1994, 1995a, 1995b); however, because the waters off California, Oregon and Washington are the primary feeding destination of the whales observed in Baja California and the mainland coast, the migratory destination of the whales seen around the Revillagigedo Islands is still unknown (Urbán et al. 1987; Urbán et al.[3]).

Previous estimates of humpback whale abundance in Mexican waters are the following: 500–600 for Socorro Is. (Campos, 1987); 200–400 for Isabel Is. (Alvarez, 1987); 600–700 for the mainland coast (Alvarez et al., 1990); and 1200–1700 for all the Mexican Pacific (Urbán et al., 1989). However, it is recognized that these estimates were based on limited data and on assumptions that generally were not tested.

In our study we present an analysis of photographic data obtained during the winter breeding and calving seasons from 1983 to 1993 in the different assembly areas of the Mexican Pacific. We use this analysis to calculate reliable independent estimates of abundance of humpback whales for the coastal and the Revillagigedo stocks.

[1] Calambokidis, J., G. H. Steiger, J. Straley, T. J. Quinn II, L. M. Herman, S. Cerchio, D. Salden, M. Yagamuchi, F. Sato, J. Urbán R., J. K. Jacobsen, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladrón de Guevara P., S. A. Mizroch, L. Shlender, K. Rasmussen. 1977. Abundance and population structure of humpback whales in the North Pacific basin. Final Rep. to Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, La Jolla, CA, 72 p.

[2] Urbán R., J., J. C. Salinas V., A. Guillén G., and E. Vázquez M 1997. La ballena jorobada *Megaptera novaeangliae* en al Península de Baja California Sur, México. Final Report to the Biodiversity National Commission (CONABIO). Contract H035, 41 p.

[3] Urbán R., J., A. Jaramillo L., A. Aguayo L., Paloma Ladrón de Guevara P., M. Salinas Z., C. Alvarez F., L. Medrano G., J. Jacobsen, K. C. Balcomb, D. E. Claridge, J. Calambokidis, G. H. Steiger, J. M. Straley, O von Ziegesar, S. Mizroch, .M. Dahlheim, J. M. Waite, J. D. Darling, and C. S. Baker. 19xx. Migratory destination of the Mexican Pacific humpback whales. Universidad Autónoma de Baja California Sur, Ap. Post. 19-B, La Paz, Baja California Sur, Mexico.

Figure 1

Study area showing, by shading, the distribution of the Revillagigedo and coastal stocks.

Materials and methods

Individual identification

Humpback whales were individually identified from photographs taken by different institutions from approximately December to March, along the mainland coast of Mexico (1983–92), from mid-January to March in Baja California (1987–93), and at the Revillagigedo Archipelago (1986–92) (Table 2).

Although photo-identification data have been available for the coastal stock since 1983 and for the Revillagigedo stock since 1985, efforts before 1986 were limited in time and space, and also lacked continuity. Beginning in 1986, surveys were conducted off Socorro Island for the Revillagigedo stock, and near San José del Cabo or the mainland coast (or both) for the coastal stock. No data were obtained for either Revillagigedo or the mainland in 1993.

The whales were identified individually through photographs of the black and white pigmentation patterns on the ventral surface of their flukes (see Katona and Whitehead, 1981). Photographs were obtained with 35-mm cameras equipped with 200–300 mm lenses. Although the film used varied by region and season, most photographs were taken with black and white Kodak Tmax 400 ISO pushed to 1600 ISO, ensuring shutter speeds as high as 1/1000 of a second.

On the basis of focus, angle, and light conditions, all fluke photographs were judged to be either good, fair, or of poor quality; only photos in the first two categories were included in this study. Within these quality levels, the whales showed at least 50% of each fluke at a sufficiently vertical angle to allow the shape of the trailing edge to be distinguished. Calves were excluded from the analysis owing to their tendency to show changes in pigmentation patterns during the first year of life (Carlson et al., 1990). Selected photographs were compared visually by at least three persons with experience in matching humpback whales flukes photographs from both Universidad Nacional Autonoma de Mexico and Universidad Autonoma de Baja California Sur.

Abundance estimation

Abundance estimates were obtained by using an eight-year period for the coastal stock, from 1986 to 1993, and a seven-year period for the Revillagigedo stock, from 1986 to 1992.

Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. The time span of the study was seven years; consequently, although calves were not included in the analysis, it is inevitable that additions

Table 2

Study periods and data sources for each of the regions. UNAM = Universidad Nacional Autonoma de Mexico; UABCS = Universidad Autonoma de Baja California Sur; CWR = Center for Whale Research; CS =Cousteau Society.

Region	Season	Study period	Source
	1986	20 Dec 85–4 Mar 86	UNAM
	1987	25 Dec 86–20 Mar 87	UNAM
	1988	22 Jan 88–8 Feb 88	UNAM
	1989	24 Jan 89–5 Mar 89	UNAM
	1990	25 Nov 89–21 Mar 90	CWR, UABCS, UNAM
	1991	28 Nov 90–26 Feb 91	UNAM
	1992	26 Dec 91–6 Mar 92	UNAM
Baja California Peninsula	1987	10 Feb 87–5 Mar 87	CWR, UABCS
	1988	6 Feb 88– 8 Mar 88	CWR, UABCS
	1989	23 Jan 89–25 Mar 89	CWR, UABCS
	1990	20 Feb 90–31 Mar 90	CWR, UABCS
	1991	24 Jan 91–23 Mar 91	UABCS
	1992	20 Jan 92–2 Apr 92	UABCS
	1993	15 Jan 93–5 Apr 93	UABCS
Revillagigedo Archipelago	1986	16 Jan 86–20 Feb 86	UNAM
	1987	20 Jan 87–5 Mar 87	UNAM
	1988	1 Feb 88–9 Mar 88	UNAM
	1989	16 Jan 89–7 Mar 89	UNAM
	1990	31 Jan 90–20 Mar 90	UNAM
	1991	15 Jan 91–25 Apr 91	UNAM
	1992	25 Apr 92–7 May 92	UNAM, UABCS, CS

to the population were occurring in the form of animals born in previous years that became identifiable as they grew. Also, some individuals died. Because we would therefore expect to be studying an open population, we chose the Jolly-Seber mark and recapture model. One of the critical assumptions of this method is the highly unlikely condition that all animals have the same capture probabilities at the moment of the sample (Seber, 1982). If heterogeneity in capture probabilities is present, the open population models will underestimate population size to a greater extent than closed population models (Carothers, 1973; Pollock et al., 1990). Given that there was no way to account for such problems with open population models (Hammond, 1986), we decided to use closed population models to test for variations in capture probabilities.

Closed population estimates were obtained and assumptions were tested by using the software program CAPTURE developed by Otis et al. (1978), which included an algorithm to select the appropriate model after the hypothesis testing procedure. The conceptual basis for this selection procedure is a tradeoff between precision and bias. If a simple model, such as the null model M_0 in Otis et al. (1978), is used to estimate parameters from data that violates in any way the assumption of equal capture probability, then significant biases are introduced in parameter estimates and sampling variances will be artificially small. On the other hand, if a more complex model is used, such as M_{th} of Otis et al.. (1978), that allows capture probabilities to vary with time and among individuals, biases may be reduced but the sampling variance will be greater than it should be. The selection procedure takes into account the individual goodness-of-fit tests performed for specific models on the data and the confrontation of related models (i.e. where one model is a particular case of a general one). The significance levels for all these tests are combined in a standard discriminant analysis and the resulting statistic is standardized so that its value ranges from 0 to 1, 1 being the score that indicates the appropriate model (Otis et al., 1978).

The basic or null model M_0 can be applied to the general case of multiple recaptures in a closed population, where all animals have equal capture probabilities, and where this probability remains constant in time. The model that allows the capture probability to vary in time, simultaneously permitting individuals to have unequal capture probability (Chao et al., 1991: model M_{th} in Otis et al., 1978) was selected for estimation of both stock sizes. In addition,

abundance was also estimated for the coastal stock by using the model that only allows relaxation of the requirement for constant capture probability in time (Darroch, 1958: model M_t in Otis et al., 1978). Model M_{th} provides the estimator of population size for a situation where capture probabilities vary in time and among individuals. Model M_t provides the estimate of population size when capture probabilities are the same among individuals but vary in time (Otis et al., 1978).

Outputs from CAPTURE were used only as a "screening technique," as suggested by Menkins and Anderson (1988) to investigate departures from the assumption of equal catchability. The test for population closure within CAPTURE was ignored because its power is low (Otis et al., 1978).

Open population estimation was done through the software program RECAP[4] This program provides estimates of parameters under the basic Jolly-Seber model where all individuals have equal capture probabilities and survivorship, but these were allowed to vary between sampling occasions. Also, it incorporates a modification of the Jolly-Seber model (modified J-S model) that constrains estimates to feasible values, stabilizing them and providing more reliable confidence intervals (Buckland, 1980). Open population estimates were also obtained by using the software program JOLLY described by Pollock et al. (1990). Of particular interest is the goodness-of-fit tests performed for this program to investigate how well our data are explained by the Jolly-Seber model or any of the variants included in the program. The results obtained under such variants were also very useful because they allowed for the estimation of more precise parameters when either capture probabilities or survivorship (or both) were kept constant. Even in the case when the more general Jolly-Seber model was chosen (model A), observation of survivorship estimates under model 2 (temporary trap response model) were useful to look for the amount of transit within the areas occupied by each stock.

Table 3

Number of humpback whales identified in Mexican waters from 1986 to 1993.

Region	1986	1987	1988	1989	1990	1991	1992	1993
Coast								
Animals caught	74	71	74	83	218	109	180	92
Newly caught	74	65	61	67	174	91	140	61
Revillagigedo								
Animals caught	26	41	73	106	48	189	36	
Newly caught	26	37	64	86	33	143	23	

Table 4

Estimates of population size (N) with closed population models (see "Materials and methods" section for descriptions of the models).

Model	N	95% CI	Capture prob. P
Coastal stock			
M_o	2039	1728–2194	0.05
M_t[1]	1828	1660–2076	0.06 average
M_{th}[1]	2188	1861–2612	0.05 average
Revillagigedo stock			
M_o	1078	807–1169	0.0687
M_t	874	762–1020	0.084 average
M_{th}[1]	1308	1043–1684	0.057 average

[1] Selected models

Results and discussion

Photo identification

A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. Of the total, 733 individuals were observed in the area occupied by the coastal stock, 412 in Revillagigedo, and 39 in both areas (a summary of the number of individuals identified in each area is provided in Table 3).

Abundance estimation

The closed population estimators showed that heterogeneity and variations in capture probabilities in time are present in both stocks. However, the confidence intervals built for models M_t and M_{th} overlap to a greater extent in the coastal estimates than in the Revillagigedo estimates, indicating that both models M_{th} and M_t are equally good for the coastal stock (Table 4). These relatively small capture probabilities estimated with the closed models are consistent with a positive bias in the population size estimates because, as will be discussed, the populations were open through the period of study. Therefore, the closed population models were useful in showing that the assumption of equal catchability is not met.

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Table 5

Estimates of population size (N) with the program JOLLY, model A (general) (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock[1]			
1987	771	119–1424	0.08
1988	484	215–753	0.14
1989	791	382–1220	0.10
1990	1247	682–1811	0.17
1991	1660	610–2712	0.06
1992	1702	488–2917	0.10
Average	1109	793–1425	0.11
Revillagigedo stock[2]			
1987	134	13–256	0.25
1988	367	125–609	0.18
1989	593	288–897	0.17
1990	456	179–733	0.10
1991	1569	−140–3277	0.12
Average	623	268–980	0.16

[1] χ^2 Goodness-of-fit model A $x = 5.968$ $P = 0.8754$
χ^2 Goodness-of-fit model 2 $x = 1.132$ $P = 0.8892$
[2] χ^2 Goodness-of-fit model A $x = 13.23$ $P = 0.0667$
χ^2 Goodness-of-fit model 2 $x = 0.448$ $P = 0.799$

Table 6

Estimates of population size (N) with the program RECAP, modified Jolly-Seber model (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock			
1987	822	425–1142	0.09
1988	580	327–931	0.13
1989	825	519–1229	0.10
1990	1120	824–1613	0.19
1991	1813	1168–2686	0.06
1992	1813	918–2505	0.10
Average	1162	889–1406	
Revillagigedo stock			
1987	167	49–484	0.25
1988	414	215–691	0.18
1989	610	388–825	0.17
1990	606	359–891	0.08
1991	914	590–1193	0.21
Average	642	373–677	

The Jolly-Seber analysis indicated that the open population model explained in a better way the data for both Revillagigedo and coastal stocks (Table 5). In the Revillagigedo stock the goodness of fit χ^2 test on model A (general model) did not reject the null hypothesis (P=0.0667), but the result showed that data are better explained (P=0.799) by model 2 (temporary trap response model), assuming that survival rates of newly captured animals differ from those of previously captured animals. In other words, this test indicates that some animals may have moved into the capture site and once captured, they could have left and even re-entered the sampling area. This inference an be supported by the fact that data for this stock were collected only in Socorro Island and that some animals may have a preference for anther island, such as Clarion, far away from the sampling area (Fig. 1). For the coastal stock, the goodness-of-fit χ^2 tests indicate that the model A (P=0.8754) and model 2 (P=0.8892) are almost equally good in explaining the data. Although sampling coverage was wider for this stock, allowing a better collection of photographs for moving animals, this problem still remained, but had a smaller effect on the estimates.

Having accepted that the Jolly-Seber model explained the data well for the two stocks, population-size estimates were obtained with the software program RECAP. Results show that the modified estimator (modified J-S model) provided more stable estimates and narrower and more realistic confidence intervals (Table 6).

Because capture probabilities are larger than those obtained by the closed population methods, and considering that the Jolly-Seber estimates may be negatively biased given heterogeneity, population size are likely overestimated by the closed population methods.

In light of the above arguments, we conclude that the best estimates of population size for the Mexican stocks, using the data at hand, are those provided by the modified Jolly-Seber model of program RECAP. Estimates obtained with closed population methods are not recommended when data are pooled for the whole extension of the study; however, it may be worth obtaining estimates with pairs of years with models testing for heterogeneity and capture probabilities varying with time, although certain information and precision may be sacrificed.

Estimates for each year show an apparent trend towards increase for both stocks. Such a trend was considered an artifact of a reduction in the bias caused by heterogeneity in capture probabilities after sample size increased with time. Consequently, we consider that the best estimates for the stock sizes were those obtained for the last years and are 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

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Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987

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Abstract.—A two-ship survey of the eastern tropical Pacific collected surface plankton samples during El Niño in August–November 1987. Although the diversity of cephalopods in these samples was low, cephalopod abundance was extremely high. Most of the cephalopods collected were rhynchoteuthion paralarvae of an ommastrephid squid, either *Dosidicus gigas* or *Sthenoteuthis oualaniensis*. High abundances (hundreds of paralarvae in a 15-min tow) were concentrated in a band parallel to the coast, 740–900 km off Central America. This band of high abundance was approximately coincident with the 29°C surface isotherm. Maximum abundance (>12,000 rhynchoteuthions in a 15-min tow) was four orders of magnitude greater than background levels and an order of magnitude greater than any other report of cephalopod abundance. Based on flowmeter readings from the sampler, the anomalous abundance was not a sampling artifact. Size-frequency analysis indicates that this patch cannot be explained as a result of recent hatching from an egg mass. This abundance may have resulted from warm El Niño waters, aggregation by convergence of surface currents, or the interaction of these factors during the squid's spawning season.

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Reports of the effects of El Niño/Southern Oscillation have been widespread in both scientific literature and popular news media. Shifts in distribution and decreases in abundance of marine animals resulting from El Niño have received much attention. Cephalopods are important components of the marine food web, as well as the targets of commercial fisheries. I report here on the serendipitous collection of squid paralarvae during El Niño 1987 at abundances an order of magnitude higher than any previously known.

Materials and methods

A two-ship survey for a visual census of marine mammals was conducted in the eastern tropical Pacific Ocean during August–November 1987. During four cruise legs, the NOAA Ship *David Starr Jordan* surveyed the area between the equator—19°N and 79–121°W, while the NOAA Ship *MacArthur*, also in four legs, covered the region westward of the *Jordan* survey to 148°W and southward to 11°S. Surface plankton samplers (Manta nets; Brown and Cheng, 1981) were towed by both ships almost every day after sunset to collect fish larvae. Surface temperature was measured by bucket thermometer concurrently with each plankton tow. The distance of each tow was estimated by a flow meter mounted below the net. Extremely high numbers of cephalopod paralarvae were found in some of these samples when they were sorted for ichthyoplankton after the conclusion of the cruises.

Results

The diversity of cephalopods in these samples was quite low; only 15 species were identified and >99% of the 15,052 cephalopods collected were a single species of the squid family Ommastrephidae (Table 1). Ommastrephid paralarvae are distinctive and are referred to as rhynchoteuthions because the two tentacles (as opposed to the eight arms) are fused throughout the early life history. Throughout the entire surveyed region, abundance of paralarval ommastrephids, measured as number of rhynchoteuthions collected per 15-min tow, generally was 0–10 squids per tow. Maximum abundance (22 stations with 20–>100 rhynchoteuthions/tow) was found about 740–900 km offshore in a band parallel to the coast of Central America (Fig. 1A). Within this band at three stations during two separate legs, 379, 461, and 12,354 rhynchoteuthions were collected, respectively. Although most of the stations in this band were sampled by the *Jordan*, the northeasternmost *MacArthur* stations were in the eastern end of

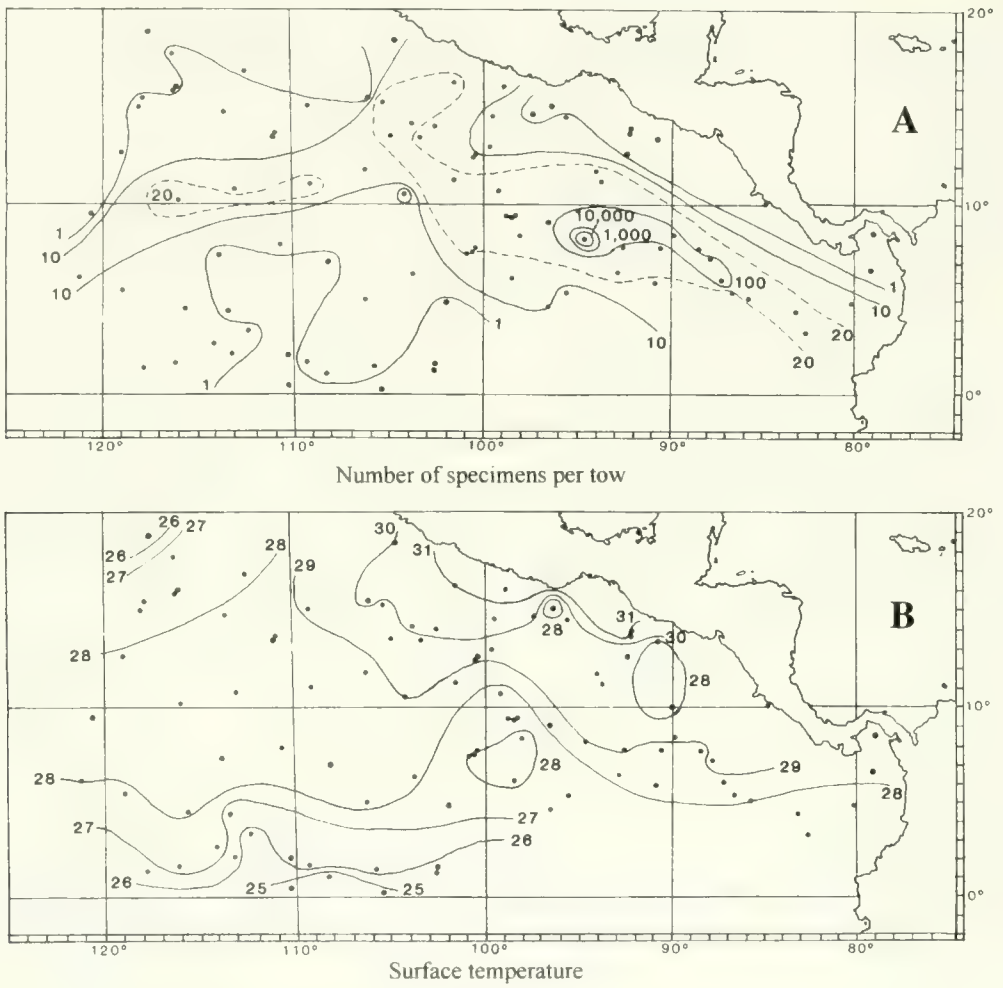

Figure 1

NOAA Ship *D.S. Jordan* cruise 8710, August–November 1987: (**A**) sampling locations and isolines of abundance for rhynchoteuthion squid paralarvae; (**B**) surface isotherms (°C).

the band. A secondary patch of abundance (five stations with 20–90 rhynchoteuthions/tow) was sampled by the *MacArthur* farther to the west (9–13°N, 121–135°W) and appeared to be a westward extension of the band of peak abundance.

The primary band of maximum abundance was approximately coincident with the 29°C surface isotherm (Fig. 1B). Peak abundance was found in the vicinity of a very productive oceanographic upwelling feature known as the Costa Rica Dome (Li et al., 1983). The secondary patch of abundance was in an area with surface temperatures in the mid-28°C range. It may be associated with a westward extension of the Costa Rica Dome, termed the countercurrent ridge (Fiedler et al., 1991). A plot of abundance versus surface temperature shows a clear peak between 27.5° and 31.0°C (Fig. 2). The three stations with highest abundances were all in areas of 29.0–29.5°C surface temperatures (see vertical arrows in Fig. 2). Abundance tapered off late in the survey although surface temperatures remained above 27.5°C (Fig. 3), within the optimum range indicated by peak abundance.

In addition to a biological-oceanographic pattern of abundance, two other alternatives could explain the pattern described here: 1) it could represent concentrated patches of recent hatchlings from isolated egg masses; or 2) it could result from sampling error associated with changes in towing characteristics of the samplers (e.g. speed, duration).

To address alternative 1, I examined size-frequency distributions based on dorsal mantle lengths (DML), both within individual samples and in the total pooled population. For samples with >100 specimens, I measured a subsample of 100. I separated the stations into dusk tows (within one hour after local sun-

Table 1

Cephalopods collected by Manta-net surface zooplankton samples during the two-ship survey of the eastern tropical Pacific, August–November 1987.

	Ship		
	Jordan	*MacArthur*	Total
Ommastrephidae	14,445	495	14,950
Argonauta sp.	16	36	52
unid. squid	9	3	12
Liocranchia sp.	1	9	10
Abraliopsis sp.	9	0	9
Onykia? sp.	4	2	6
Chiroteuthis sp.	3	0	3
Pterygioteuthis sp.	2	0	2
Chtenopteryx sp.	1	1	2
Enoploteuthis? sp.	1	1	2
Abralia? sp.	1	0	1
Thysanoteuthis rhombus	1	0	1
Cranchia scabra	1	0	1
Leachia sp.	1	0	1
Octopodidae	0	1	1
Total	14,495	548	15,043

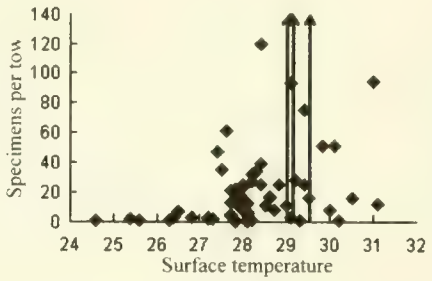

Figure 2

Rhynchoteuthion squid paralarval abundance plotted against surface temperature for NOAA Ship *D.S. Jordan* cruise 8710. Vertical arrows represent samples with maximum numbers of paralarvae.

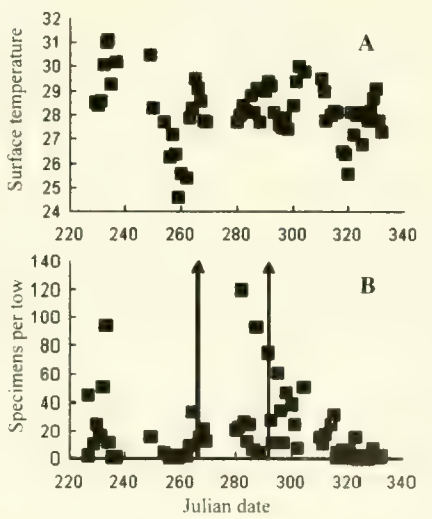

Figure 3

Relationships among water temperature, squid abundance, and date for NOAA Ship *D.S. Jordan* cruise 8710: (**A**) surface temperature plotted against Julian date; (**B**) rhynchoteuthion squid paralarval abundance plotted against Julian date. Vertical arrows represent samples with maximum numbers of paralarvae.

set) and night tows to determine the contribution of diel variability, from either visual avoidance of the net or vertical migration by larger animals, to the size distribution. The overall size distribution was skewed toward the size of newly hatched animals, with the model length 1.0–1.5 mm DML. The size range in dusk samples was 0.5–3.5 mm DML (Fig. 4A). A small second group of larger squid 3.5–8.5 mm DML (modal length ca. 6.0–6.5 mm DML) not present in dusk tows was collected at night in addition to the smaller paralarvae (Fig. 4B). Some stations, such as *Jordan* station IV-05 (Fig. 4D), included only very small squid 1–2 mm DML, as might be expected from a hatching event. The greatest abundance, however, at station III-62, was characterized by a broader range of lengths (Fig. 4C) with a larger modal size of 2.0–2.5 mm DML. On the basis of analysis of growth rings in statoliths from Hawaiian *S. oualaniensis*, a 2.5-mm-ML paralarva is ca. 20 days old (Bigelow, 1991). I therefore conclude that this very high abundance did not result from the net happening upon an egg mass, either just before or just after hatching, but instead an aggregating mechanism must be responsible for this patch.

I examined the second alternative by calculating the variability in flow meter revolutions among tows. The mean and standard deviation for this estimate of sampling efficiency were 2771 and 645, respectively. None of the three outliers from this distribution (one high and two very low) collected >20 rhynchoteuthions. All of the samples with abundances >40 rhynchoteuthions came from tows with 2612–2947 revolutions. Although this parameter can be used to estimate the volume of water filtered by the sample, I did not do this because assumptions about the orientation of the net mouth with respect to the sea surface are required for surface samples and this orientation can change greatly with sea

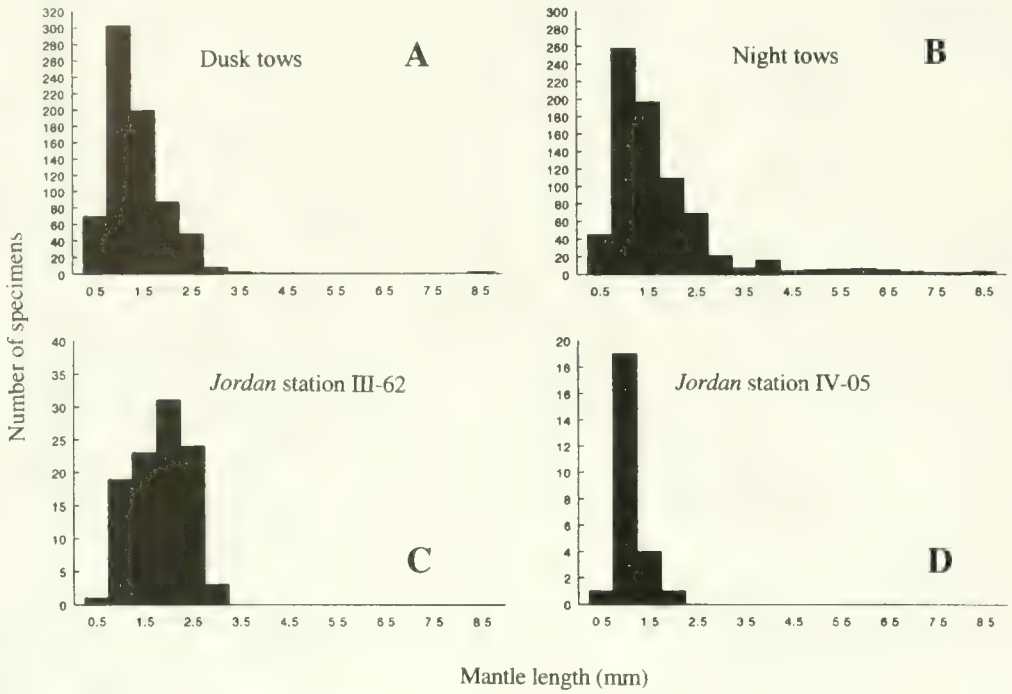

Figure 4

Size-frequency distributions for ommastrephid paralarvae. All specimens were measured from samples that collected <100 rhynchoteuthions. A subsample of 100 specimens was measured from samples containing >100: (**A**) pooled distribution for all dusk tows (samples collected <1 h after local sunset); (**B**) pooled distribution for all night tows (samples collected >1 h after local sunset); (**C**) lengths of 100 specimens from the station that collected maximum abundance; (**D**) example of size-frequency distribution expected from a station that sampled a recent hatching event.

state. The low variability of flow meter counts indicates that observed abundances did not result from sampling artifacts.

Discussion

Aside from the band of high rhynchoteuthion abundance parallel to the coast and coincident with the 29°C isotherm, these collections are not unusual for surface samples of cephalopod paralarvae. The abundance of other cephalopods with paralarvae typically found at the surface, such as *Argonauta*, was not exceptional. Unusually high abundances in these samples were found only in the paralarvae of ommastrephid squids.

The Humboldt squid, *Doscidicus gigas*, is an ommastrephid sufficiently abundant in this area to support commercial fisheries, but descriptions of the paralarvae of this species are not adequate to identify them with confidence. However, the general morphology, morphometrics, and chromatophore patterns of the paralarvae reported here are consistent with those of another widely distributed and abundant ommastrephid, *Sthenoteuthis oualaniensis*, whose paralarvae have been described from off Hawaii (Harman and Young, 1985). It is not possible at this time to be certain which of these species composed the high abundances reported here. Although natural spawning has not been observed directly for either of these species, ommastrephids are known to spawn large egg masses that are gelatinous and pelagic and are very difficult to collect with nets. Spawning aggregations of *S. oualaniensis* and other ommastrephids have been located in other areas. It seems reasonable to assume that either species may aggregate in the study area to produce egg masses.

No information is available on the abundance of these squid paralarvae in subsurface waters of this region. The highest abundance of *S. oualaniensis* in Hawaiian waters is found in the mixed layer from the surface to 20 m depth (Young and Hirota, 1998). Surface abundance therefore appears to be a reasonable indication of overall paralarval distribution of this species. Furthermore, the depth of maximum zooplankton abundance in the eastern tropical

Pacific is generally limited by an oxygen minimum layer beneath the thermocline (Saltzman and Wishner, 1997). Thus, the distribution of these shallow-living paralarvae may have been compressed toward the surface by the oxygen-minimum layer.

Expendable bathythermograph measurements by the *Jordan* during this period showed the mixed-layer depth to be 20–40 m, except where the thermocline was depressed within an anticyclonic eddy located very close to the stations with maximum squid abundance (Hansen and Maul, 1991). Convergence of surface currents associated with the downwelling that depresses the thermocline could aggregate surface plankton such as these paralarvae (Bakun and Csirke, 1998). Although the area of maximum abundance was near the Costa Rica Dome, an upwelling feature where the thermocline typically shoals from 60 m to 30 m depth (Balance et al., 1997), thermal topography in this area was anomalously flat during El Niño of 1987 (Fiedler et al, 1992).

A few other records of cephalopod distribution and abundance are known from this region. In an extensive multicruise survey of the eastern tropical Pacific in 1967–68 (Okutani, 1974), few *S. oualaniensis* or other ommastrephids were collected. Similarly, in a cruise in this region from October 1969 through February 1970, during which surface zooplankton were sampled, no large numbers of paralarvae were encountered, although the most abundant cephalopod family sampled was the Ommastrephidae (Ueynagi and Nonaka, 1993).

Typical numbers of cephalopod paralarvae taken in zooplankton samples worldwide number 0 to perhaps 20 squids per sample, usually about 1–5 squids (Vecchione, 1987). The highest abundance previously reported anywhere of which I am aware was almost 1000 loliginid paralarvae in a 15-min surface plankton tow in the western North Atlantic (Vecchione et al., 1986). The maximum abundance found in the present study was over an order of magnitude greater than that.

The samples reported in this study were collected during the peak of a moderate El Niño event (McPhaden and Hayes, 1990). Surface temperatures in the area averaged 3.5°C warmer than during the same period of the following year (Fiedler et al., 1992). The temperature distribution of these samples indicates that high abundances of rhynchoteuthions would not be expected at temperatures <27.5°C. Therefore, warm El Niño waters probably were the primary reason for the high abundance of squid paralarvae found here. These abundant surface-dwelling paralarvae may have been concentrated to extraordinary densities by convergent surface currents in the vicinity of an anticyclonic eddy. Seasonal occurrence is likely important, because surface temperatures remained high until the end of these cruises, whereas squid abundance decreased dramatically during the final 30 days. The sampling fortunately was conducted during the season when these squid were hatching.

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Early life history stages of the whitetip flyingfish, *Cheilopogon xenopterus* (Gilbert, 1890) (Pisces: Exocoetidae)

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Abstract.—The whitetip flyingfish, *Cheilopogon xenopterus*, is an epipelagic resident of tropical and subtropical eastern Pacific waters. Its eggs are spherical, average 1.8 mm in diameter, and have an homogeneous yolk and no oil globule. About 53 filaments averaging 1 mm in length are evenly distributed on the chorion. The notochord flexes, fin-ray formation is nearly complete, and the characteristic larval pigmentation pattern is established prior to hatching at a larval length of about 2.8–3.3 mm. Larvae hatch with pigmented eyes, functional mouth, and little remaining yolk. Pectoral- and pelvic-fin rays initially are short but elongate rapidly to ca. 25–50% and 20–40% of body length, respectively. A pair of mandibular barbels form at about 4 mm and fuse mesially at about 8 mm. Scales begin to form along the lateral line at about 13–14 mm and cover the body by 26 mm.

The characteristic pigment pattern, visible through the early juvenile stage, consists of the following: melanophores scattered over the mid- and hindbrain, continuing posteriorly as two rows (increasing to four or more rows) along the dorsal margin; a row of melanophores on the horizontal septum of the tail (after hatching); a patch on each side over the hypural area; and two rows along the anal-fin base. Internal pigment is present on the mid- and hindbrain, over the gut, and over the notochord. The pectoral and pelvic fins are sparsely pigmented at hatching and become increasingly pigmented with growth. A barred pigment pattern begins to develop on the body at about 8 mm and by the juvenile stage about six bars are present.

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Flyingfishes, surface-oriented residents of all warm oceans, are well known for their ability to leap from the water and glide over long distances. Flyingfishes can be abundant locally, many are attracted to light, and the gustatory quality of their flesh is generally good (Heemstra and Parin, 1986; Gillett and Ianelli, 1991; Parin, 1995). Directed fisheries for flyingfish currently exist, primarily in parts of the Indo-West Pacific and Caribbean; few such fisheries exist elsewhere (Gillett and Ianelli, 1991; Oxenford et al., 1995; Parin, 1995).

The family contains eight or nine genera and about 50–60 species (Nelson, 1994; Dasilao et al., 1996); nearly half the species are in the genus *Cheilopogon* (Heemstra and Parin, 1986). Eggs have been described for nine *Cheilopogon* species (Barnhart, 1932; Hubbs and Kampa, 1946; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Parin and Gorbunova, 1964; Kovalevskaya, 1965; Gibbs and Staiger, 1970; Vijayaraghavan, 1975; Shigonova and Kovalevskaya, 1991; Watson, 1996), and at least some larval stages are known for 16 species (Hildebrand and Cable, 1930; Barnhart, 1932; Breder, 1938; Hubbs and Kampa, 1946; Imai, 1959, 1960; Gorbunova and Parin, 1963; Kovalevskaya, 1965, 1975, 1977, 1982; Vijayarhagavan, 1975; Chen, 1987, 1988; Shigonova and Kovalevskaya, 1991; Belyanina, 1993; Parin and Belyanina, 1996; Watson, 1996). The purposes of this paper are to provide a description of the egg, larval, and early juvenile stages of the endemic eastern Pacific species *Cheilopogon xenopterus* (Gilbert, 1890) and to compare these briefly with the early stages described for other *Cheilopogon* species in the eastern Pacific.

Materials and methods

Descriptions are based on 20 eggs and a size series of 45 larvae (2.8–22.8 mm) and 8 juveniles (25.9–44.8 mm). Neustonic eggs and larvae and three of the juveniles were collected with Manta nets (Brown and Cheng, 1981) during Marine Mammals Division (Southwest Fisheries Science Center) dolphin surveys in the eastern tropical Pacific (Thayer et al., 1988a, 1988b; Lierheimer et al., 1989, 1990; Philbrick et al., 1991, 1993). The Manta samples were taken nightly from late July through early November or December, 1987–90, and 1992, between about 2–16°N and east of about 115°W. A few juvenile and adult specimens of *C. atrisignis*, *C. dorsomaculata*, *C. furcatus*, *C. papilio*, *C. spilonotopterus*, and *C. xenopterus*, radiographed to make fin-ray and vertebral counts for comparison with counts from series specimens, were obtained from the Scripps Institution of Oceanography Marine Vertebrates Collection (SIO).

Eggs, larvae, and juveniles (except those used exclusively for radiography) were measured to the nearest 0.04 mm by using a Wild M-5 binocular microscope equipped with an ocular micrometer. Dimensions measured for eggs included chorion diameter, maximum yolk diameter, and lengths of the shortest and longest intact chorionic filaments, and for larvae and juveniles, body length (BL), preanal length (PAL), head length (HL), snout length (SnL), barbel length (BbL), eye diameter (ED), head width (HW), body depth (BD), and lengths of the pectoral (P_1L) and pelvic (P_2L) fins. All these dimensions, except chorionic filament length (measured along the axis of the filament from its point of attachment on the chorion to its free tip), are defined by Moser (1996). Larval lengths refer to formalin-preserved body length. All descriptions of pigmentation refer solely to melanistic pigment.

One late embryo (3.3 mm) dissected from the egg and eight larvae (2.9–16.8 mm) were cleared and stained with alcian blue and alizarin red S according to the method of Taylor and VanDyke (1985) to elucidate the development of the axial skeleton and fins and to aid in making counts. Illustrations were made with a Wild M-5 microscope equipped with a camera lucida.

Identification

Specimens were identified by the series method. A size series of larvae and juveniles, linked by shared morphological, meristic, and pigmentation characters, was traced down to recently hatched larvae from juveniles that could be identified by using known juvenile and adult characters. The smallest larvae shared a pigmentation pattern with late-stage embryos that allowed identification of the eggs.

Of the eight flyingfish genera in the eastern tropical Pacific (Parin, 1995; Dasilao et al., 1996), only *Cheilopogon* has paired mandibular barbels during at least part of the larval and juvenile stages (Parin, 1961a, 1961b; Collette et al., 1984). (*Parexocoetus brachypterus* develops a pair of mandibular barbels, and a small beak as well, during the juvenile stage: Collette et al., 1984.) Of the nine *Cheilopogon* species in and near the area (Table 1; Parin, 1995), larvae are known for five: (*C. atrisignis*: Chen, 1987, 1988; *C. furcatus*: Hildebrand and Cable, 1930; *C. heterurus hubbsi*: Barnhart, 1932; Watson, 1996; *C. pinnatibarbatus californicus*: Hubbs and Kampa, 1946; Watson, 1996; and *C. spilonotopterus*: Kovalevskaya, 1977; Chen, 1987, 1988). All five differ from the series treated here. *Cheilopogon rapanouiensis* was eliminated from consideration by its higher vertebral, pectoral-fin ray, and predorsal scale counts (45–46 vs. 43, 16–17 vs. 13–15, and 31–33 vs. 27–28, respectively). *Cheilopogon papilio* was eliminated because of its lower dorsal-fin ray count (9–10 vs. 12–13), usually lower pectoral-fin ray count (12–13 vs. 13–15), because of separate rather than fused barbels and much heavier pectoral- and pelvic-fin pigmentation in the juvenile stage, and because of restricted distribution in coastal waters and the lower Gulf of California (Parin, 1995). The remaining two species, *C. dorsomaculata* and *C. xenopterus*, are widely distributed in the eastern tropical Pacific (Parin, 1995), are quite similar in appearance as small (<ca. 40 mm) juveniles, and both were considered as possible identifications for the present series. Predorsal scale counts from the largest series juveniles (27–28 scales) are consistent with *C. xenopterus* and slightly high for *C. dorsomaculata* (Table 1). Pectoral-fin ray counts for series specimens having full complements of rays (>9 mm; 13–15 rays) match the range for *C. xenopterus* and fall below to within the lower half of the range for *C. dorsomaculata* (Table 1). Juvenile *C. dorsomaculata* typically have less pelvic-fin pigment than *C. xenopterus*, and in this character the larger series specimens are consistent with *C. xenopterus*. Thus, I concluded that the series is *C. xenopterus*.

Specimens examined

Listings are given as cruise and station number or SIO catalogue number, and in parentheses number of specimens and size range. Specimens listed with cruise numbers are housed at the National Marine Fisheries Service Southwest Fisheries Science Center; specimens with SIO numbers are housed at the Scripps Institution of Oceanography Marine Vertebrates Collection.

Cheilopogon xenopterus (Gilbert, 1890).

Eggs: 8910JD: 3-100 (3: 1.8–1.9 mm), 3-102 (7: 1.8–1.9 mm), 4-107 (1: 1.7 mm); 9210JD: 1-001 (4: 1.8–1.9 mm), 1-008 (4: 1.8–1.9 mm), 3-047 (1: 1.8 mm).

Larvae: 8710JD: 1-009 (1: 15.2 mm), 2-016A (1: 2.8 mm), 3-046 (6: 3.4–4.8 mm), 3-054 (1: 2.9 mm), 3-056 (1: 4.9 mm), 3-075 (1: 2.9 mm), 3-078 (2: 5.3, 14.3 mm); 8710M4: 1-003 (1: 4.1 mm); 8810JD: 2-049 (1: 8.0 mm), 3-086 (1: 7.5 mm), 3-118 (5: 8.7-13.6 mm), 4-153 (1: 8.3 mm); 8910JD: 1-015 (1: 2.9 mm), 1-019 (1: 6.4 mm), 1-021 (1: 13.7 mm), 2-056 (1: 6.8 mm), 3-104 (1: 4.8 mm); 8910M4: 1-010 (1: 12.5 mm), 1-012 (1: 3.4 mm), 4-143 (2: 9.8, 13.9 mm); 9010JD: Manta 54 (1: 13.4 mm), Manta 65 (1: 6.4 mm), Manta 74 (1: 22.8 mm); 9210JD: Manta 2 (1: 8.1 mm), Manta 9

Table 1

Selected meristic characters for the *Cheilopogon* species that occur in and near the eastern tropical Pacific Ocean. The pectoral-fin ray count includes the small, spine-like first pectoral-fin ray. Data are from Parin (1960, 1961a), Watson (1996), and counts made during this study. D = dorsal; A = anal; P_1 = pectoral; Proc.C = procurrent caudal-fin rays.

	Vertebrae			Fin rays				
Species	Abdominal	Caudal	Total	D	A	P_1	Proc. C	Predorsal scales
atrisignis	28–30	15–16	43–45	13–15	9–10	13–15	6+8	31–40
dorsomaculata	28–29	14–15	42–44	11–14	9–10	14–17	5–6+6–7	23–25
furcatus	29–31	14–15	43–46	12–14	9–11	14–18	7+6–8	27–35
heterurus hubbsi	31–33	15–17	47–49	12–14	8–11	14–16	6–7+7	28–36
papilio	28–29	14–15	42–44	9–10	9–10	12–13	4–5+6	29–33
pinnatibarbatus californicus	31–35	16–17	48–51	9–13	9–12	14–15	5–6+6–8	40–43
rapanouiensis	30–31	15–16	45–46	11–12	10–11	16–17		31–33
spilonotopterus	29	14	43	13–14	10–11	13–15	6+7	29–34
xenopterus	27–30	13–15	42–44	10–13	9–10	13–15	5–6+6–8	27–30

(1: 6.3 mm), Manta 11 (2: 4.7, 5.3 mm), Manta 19(?) (1: 8.1 mm), Manta 34 (2: 5.3, 5.6 mm), Manta 37 (1: 16.5 mm), Manta 47 (1: 6.5 mm), Manta 51 (1: 6.8 mm); SIO 63-54 (1: 18 mm).

Juveniles: 8710JD: 1-006 (1: 25.9 mm); 8810JD: 3-108 (1: 44.8 mm); 8910JD: 1-039 (1: 36.4 mm); SIO 63-31 (1: 116 mm); SIO 63-96 (1: 38.5 mm); SIO 63-105 (7: 34.5–57.0 mm); SIO 63-608 (3: 64–92 mm); SIO 64-539 (1: 62 mm); SIO 72-121 (2: 42, 45 mm); SIO 73-400 (3: 63–76 mm).

Cheilopogon atrisignis (Jenkins, 1903). SIO 79-29 (1: 52 mm).

Cheilopogon dorsomaculata (Fowler, 1944). SIO 52-399 (1: 46 mm); SIO 52-416 (6: 147–214 mm); SIO 58-318 (1: 179 mm); SIO 78-214 (1: 36.5 mm).

Cheilopogon furcatus (Mitchill, 1815). SIO 76-246 (1: 52 mm); SIO 93-89 (1: 183.5 mm FL).

Cheilopogon papilio (Clarke, 1936). SIO 58-395 (2: 65–75 mm); SIO 69-387 (2: 20, 21 mm); SIO 93-95 (2: 109, 115.5 mm).

Cheilopogon spilonotopterus (Bleeker, 1866). SIO 60-265 (1: 103 mm); SIO 69-405 (1: 39 mm).

Description of eggs

Morphology

Eggs spherical, average 1.8 mm in diameter (range 1.7–1.9 mm), have narrow perivitelline space (mean yolk diameter 1.7 mm, range 1.5–1.8 mm), homogeneous yolk, and lack oil globules (Fig. 1). Between about 42 and 64 slender filaments (mean 53) evenly distributed over smooth, transparent chorion; each attached to chorion at one end and all of similar length (mean 1.2 mm, range 0.7–1.4 mm).

Pigmentation

Chorion unpigmented, yolk colorless to pale yellow. Embryonic pigmentation first appears about midway through development (stage VIII; embryonic tail length increases from 50% to 100% HL during this stage; e.g. Moser and Ahlstrom, 1985) as one to few small melanophores dorsolaterally on midbrain area and small cluster just anterior to each pectoral-fin bud (Fig. 1B). Pigmentation increases dorsolaterally on head, forms around margins of eyes and ventrally on head in stage IX (tail > HL but < 50% yolksac length). During this stage melanophores spread posteriorly and dorsally from prepectoral clusters, forming two rows on dorsum to midway along embryonic axis, and melanophores form dorsally on developing gut, beginning posteriorly early in stage. By stage X (tail extends 50–75% of yolksac length) characteristic larval pigment pattern clearly visible, with dorsal rows extending to near end of tail, a few melanophores around margin of caudal peduncle, and two rows along base of anal fin (Fig. 1C). Near end of embryonic development (stage XI: tail extends >75% of yolksac length) melanophores fill in over central axis of head, form near distal margins of pectoral fins and proximally on caudal fin, may form near distal margins of pelvic fins (present in one of three stage-XI specimens examined), form in internal series over notochord and posteriorly under notochord, and become increasingly dense on dorsal and ventral margins near midtail. Eyes become fully pigmented during stage XI.

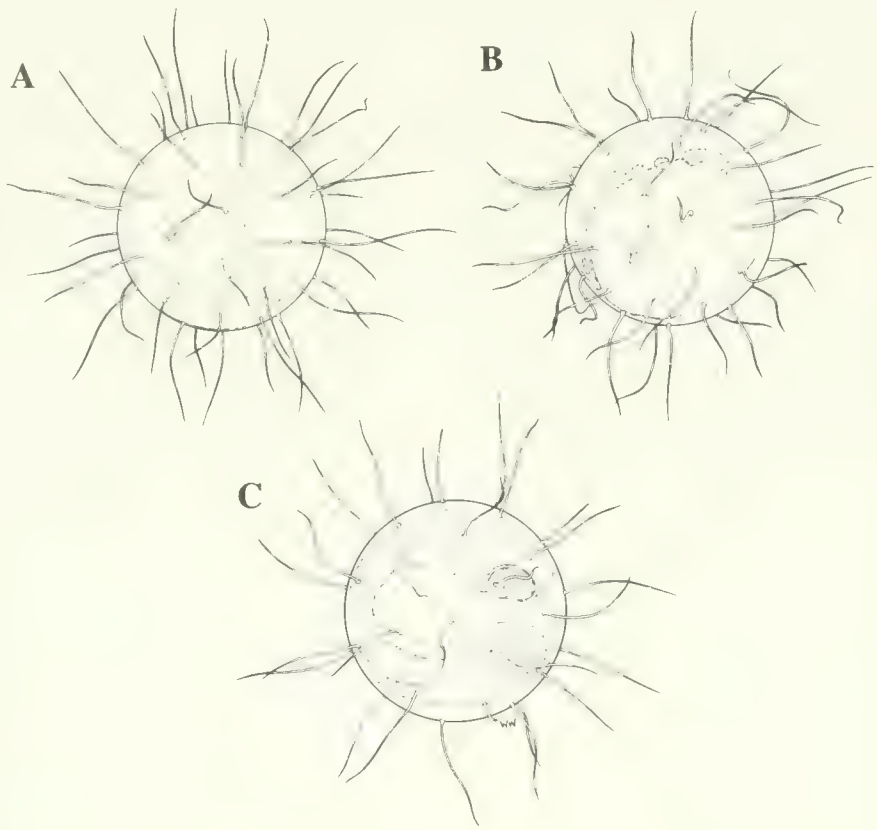

Figure 1

Eggs of *Cheilopogon xenopterus*. (**A**) stage VI, 1.8 mm (8910JD, station 3-102); (**B**) stage VIII, 1.8 mm (9210JD, station 1-008); (**C**) stage X, 1.9 mm (8910JD, station 3-100).

Description of larvae

Morphology

Larvae hatch at about 2.9–3.3 mm length and have little remaining yolk, functional mouth, fully flexed notochord, and rays forming in all fins (Fig. 2). Larvae moderately elongate, with preanal length near 80% BL at hatching, become increasingly elongate with preanal length decreasing to near 70% BL by ca. 8 mm (Table 2). Eyes initially oval (vertical axis about 70% horizontal axis), gradually becoming nearly round. Pectoral- and pelvic-fin rays initially short (near 10% BL), rapidly elongate to ca. 25–50% and 20–40% BL, respectively. Height of dorsal fin increases from about 15% BL in large larvae (15–18 mm) to about 28% BL in small juveniles (by ca. 36 mm). A pair of mandibular barbels forms at about 4 mm. Barbels originate as low, anteroventral thickening that elongates into a slender, flattened flap on each side of lower jaw. Barbels broaden, develop frilled margins, and fuse mesially at their bases by about 8.3 mm (Figs. 2–4). Scales form along lateral line beginning at about 13–14 mm and cover body by 26 mm. There are 27–30 predorsal scales and seven scale rows between dorsal-fin origin and lateral line.

Vertebral column and fin development

Notochord flexion begins during embryonic stage VIII (dorsal, anal, caudal finfolds first visible in this stage) and is completed early in stage IX. Vertebral column ossification begins soon after hatching. Neural and haemal arches and spines apparently form first, before corresponding vertebral centra. Ossification of arches apparently anterior to posterior: in 3.8-mm specimen all arches ossifying except last three neural arches, last haemal arch, and last three or four neural and haemal spines (all present as cartilage). Direction of ossification of individual arches apparently distad from base: in 3.8-mm specimen haemal arches 11–13 appear to be ossifying from near base

Table 2

Summary of measurements of *Cheilopogon xenopterus*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter (ED), eye length is given first and eye height second; *n* = number of specimens. Specimens 24.1 mm and larger were considered juveniles. PAL= preanal length; P_1L = pectoral-fin length; P_2L = pelvic-fin length HW = head width; SnL = snout length; BbL = barbel length.

BL (mm)	*n*	PAL/BL	BD/BL	HL/BL	P_1L/BL	P_2L/BL	HW/HL	SnL/HL	ED/HL	BbL/HL
2.8–4.0	9	76	24	33	28 (*n*=6)	28 (*n*=5)	69	14	42,31	0.3
		71–88	22–28	30–39	12–35	18–32	67–74	12–17	39–47, 28–34	0–3
4.1–6.0	10	72	21	30	38 (*n*=8)	38 (*n*=9)	69	17	41,33	4 (*n*=9)
		68–75	19–24	29–33	27–50	34–44	66–75	13–23	38–45, 29–35	2–10
6.1–8.0	8	70	18	26	37 (*n*=5)	30	67	17	41,34	17 (*n*=7)
		68–73	17–20	24–28	35–40	28–33	63–73	14–20	38–42, 31–37	10–24
8.1–10.0	6	69	17	24	39 (*n*=5)	35 (*n*=5)	66	17	43,36	36
		66–71	16–18	23–25	35–43	30–39	61–72	16–19	40–46, 33–42	24–48
10.1–12.0	2	68	17	22	40(*n*=1)	31	67	16	44,37	46
		68–68	16–17	22–22		30–32	67–67	16–17	43–44	39–53
12.1–14.0	5	68	15	20	42	35	71	18	46,42	49
		66–68	14–16	19–20	39–46	34–37	68–73	16–19	43–48, 39–45	39–57
14.1–16.0	2	73	16	21	48	39	73	15	47,43	65
		72–75	16–17	20–21	46–49	37–41	70–76	13–17	44–50, 42–43	59–72
16.1–18.0	2	68	16	20	50	41	74	20	45,43	71
		68–68	15–18	19–20	49–52	41–41	73–75	17–22	44–47, 41–45	59–83
22.1–24.0	1	68	15	20	58	39	71	20	46,45	61
24.1–26.0	1	69	15	19	56	39	76	18	48,47	55
34.1–36.0	1	71	16	21	65	43	70	24	38,37	43
36.1–38.0	1	72	16	20	68	44	73	17	42,44	44
38.1–40.0	1	74	15	22	72	43	67	18	36,36	43
40.1–42.0	2	72	16	22	67	42	67	21	39,40	46
		71–73	15–16	22–22	67–68	41–42	66–68	20–23	36–41, 38–42	39–53
42.1–44.0	1	71	16	22	69	43	66	20	38,37	39
44.1–46.0	1	77	19	21	72	42	79	19	43,44	53

of each haemapophysis. In 6.3-mm specimen last four neural arches and spines broadening and by 8.2 mm last six much broader than more anterior neural arches and spines. These broad posterior neural arches and spines provide the necessary attachment surfaces for the large supracarinalis posterior, flexor dorsalis, and flexor ventralis muscles (Winterbottom, 1974; Dasilao et al., 1996) which are involved in generating the strong caudal thrust required for gliding.

Ossification of each vertebra begins ventrally. As bone spreads dorsad from ventrum, ossifications also form at bases of the two neurapophyses and spread mesially and ventrad to complete centrum. Centra apparently added from anterior to posterior, but urostyle and penultimate centrum ossify before other caudal vertebrae. All vertebrae ossified by 5.2 mm (Table 3). There are 42–44 vertebrae: 27–30 abdominal and 13–15 caudal (modally 29 + 14 = 43).

Pleural ribs first visible in 6.3-mm specimen (Table 3). These ossify adjacent to parapophyses beginning at third vertebra (at second vertebra on one side in one specimen) and are added posteriorly. Epineural intermuscular bones begin ossifying in myosepta anteriorly, initially remote from vertebrae, by 8.2 mm (Table 3), and pairs added posteriorly. Ossification of each rib and epineural intermuscular bone is both mesial toward adjacent parapophysis, and distal. Full complements of both series not yet formed in largest cleared and stained specimen.

Caudal and pectoral are first fins to begin forming. Hypural elements first visible in late stage-VIII embryos, begin ossifying soon after hatching (by 2.9 mm). Retrorse basal spur forms on hypural 1 by 6.3 mm. Uroneural ossifying by 5.2 mm and epurals 1 and 2 by 6.3 mm. Epural 3 not clearly ossifying until 8.2 mm. Principal caudal-fin rays begin to form

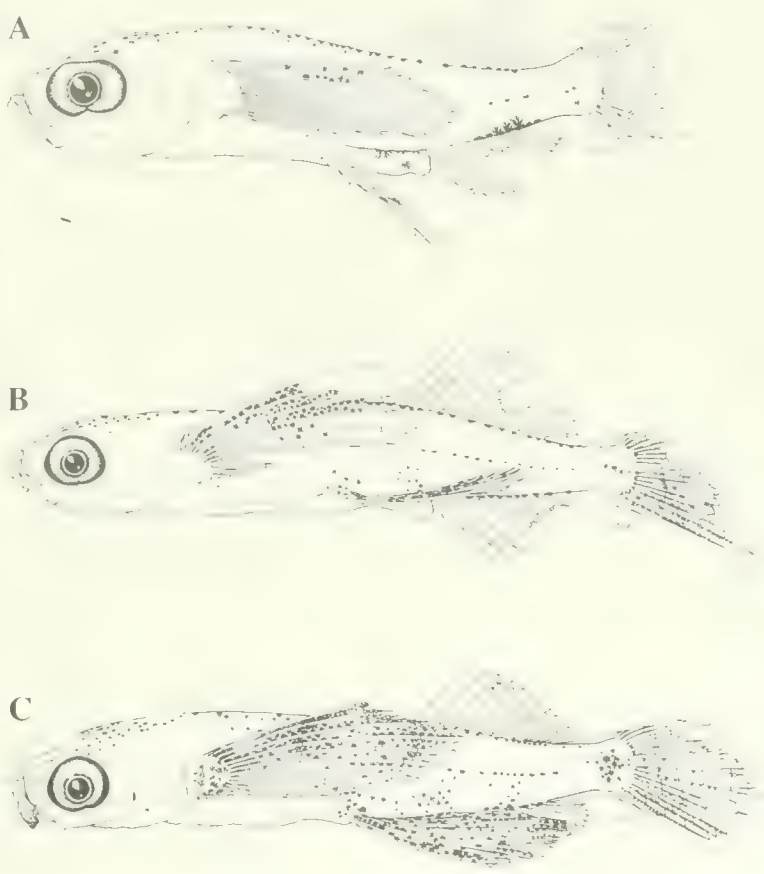

Figure 2

Larval *Cheilopogon xenopterus*, lateral view. (**A**) 3.5 mm (8710JD, station 3-046); (**B**) 8.0 mm (8810JD, station 2-049); (**C**) 8.1 mm (9210JD, station Manta 2). Fin rays shown in dotted lines are based on fins of other specimens of similar size.

during embryonic stage X (Table 3) and all 7+8 rays present at hatching. All principal rays supported by hypurals through at least 8.2 mm but by 10.5 mm lowermost principal ray partially supported by haemal spine associated with preural centrum 1. By 13.4 mm lowermost principal ray fully supported and adjacent principal ray partially supported by haemal spine, and by 16.8 mm both rays fully supported by haemal spine. Procurrent caudal-fin rays begin to form shortly after hatching (by 3.8 mm) but full complement of 5–6 dorsal and 6–8 ventral rays not attained until near end of larval development (by 16.8 mm). Caudal fin initially rounded, becomes assymetrical as lower principal rays elongate, beginning at about 5 mm.

Pectoral-fin buds form in stage-VIII embryos, almost simultaneously with beginning of notochord flexion, and upper rays form during embryonic stage X. Addition of rays is ventrad, with full complement of 13–15 rays (including uppermost small, spine-like ray) attained by 9.3 mm (Table 3). Lowermost ray quite small and nearly completely covered by scales in juveniles larger than

Table 3

Counts for cleared and stained *Cheilopogon xenopterus*. In cases where two counts are given for one category, the first value is the count from the left side, the second is from the right side. Pectoral fin-ray counts include the first small, spine-like ray. D = dorsal; A = anal; P_1 = pectoral; P_2 = pelvic; C = caudal.

	Vertebrae					Fin rays				
BL (mm)	Abdominal	Caudal	Pleural ribs	Epineural intermuscular	Branchiostegal rays	D	A	P_1	P_2	C
3.3 (embryo)	0	0	0	0	2	0	0	3	5	0+5+5+0
2.9	0	0	0	0	2	11	10	6	6	0+7+8+0
3.8	23	2	0	0	6	12	10	13	6	1+7+8+1
5.2	28	15	0	0	7	12	10	11	6	2+7+8+2
6.3	29	14	12	0	7,8	13	10	12	6	2+7+8+2
8.2	29	14	15	8	9	12	9	12	6	3+7+8+3
10.5	29	14	17	14	9	12	11	13	6	3+7+8+4
13.4	28	15	20,21	26	9	12	9	15,14	6	4+7+8+6
16.8	28	15	22	29	11	13	9	15	6	6+7+8+7

about 38 mm. Pelvic-fin buds form during embryonic stage IX, at about completion of notochord flexion. All six pelvic-fin rays apparently present at hatching.

Cartilaginous dorsal- and anal-fin pterygiophores form late during embryonic development: cleared and stained late stage-X embryo had six dorsal, five anal-fin pterygiophores. Addition and ossification of pterygiophores apparently anterior to posterior. Each pterygiophore initially is single cartilage which begins to ossify near middle of lower portion (forming proximal radial). Although pterygiophores did not stain well in smaller larvae, at least first three or four anal-fin pterygiophores beginning to ossify in 3.8-mm specimen and first five or six dorsal- and anal-fin pterygiophores in 5.2-mm specimen. By 6.3 mm all but posterior three or four dorsal proximal radials ossifying, and distal radials appear to be ossifying adjacent to fin-ray bases. About 8.2–13.4 mm separate ossifications, probably representing middle radials, form on cartilage between proximal and distal radials, but by 16.8 mm each proximal + middle radial appears to be a single ossified unit. Dorsal- and anal-fin rays begin to form in stage-XI embryos; all anal- and most dorsal-fin rays present at hatching.

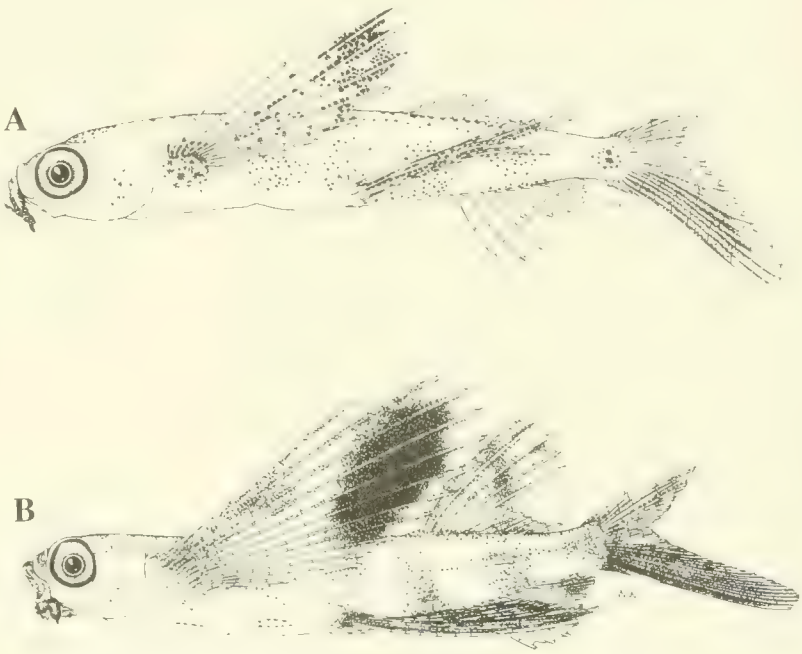

Figure 3

Cheilopogon xenopterus, lateral view. (**A**) larva, 12.5 mm (8910M4, station 1-010); (**B**) juvenile, 36.4 mm (8910JD, station 1-039). Fin rays (and fin pigment in A) shown in dotted lines are based on fins of other specimens of similar size.

Pigmentation

Most elements of basic pattern established during late embryonic development are visible throughout larval period. Principal internal elements of pattern are 1) melanophores under mid- and hindbrain (difficult to see after about 6 mm); 2) row over notochord (difficult to see after about 6 mm); 3) melanophores present around urostyle and proximally on hypurals; 4) melanophores present dorsally, dorsolaterally on gut. Principal external elements are: 1) dorsal melanophores covering mid- and hindbrain areas; 2) two somewhat irregular rows along dorsal margin of trunk and tail (increasing to four rows after about 9 mm), and melanophores in each row usually more closely spaced along posterior half of dorsal-fin base; 3) two rows along anal-fin base, commonly expanded along posterior half of fin base; 4) patch on each side over urostyle and hypural area; 5) scattered melanophores on pectoral, pelvic, and caudal fins.

Subsequent additions to internal pigmentation include melanophores spreading around sides of mid- and hindbrain and increasing in number anteriorly over notochord, forming internally on opercular area beginning at about 6–6.5 mm, and spreading ventrolaterally on gut (primarily anteriorly), surrounding gut at level of pectoral-fin bases between 12 and 18 mm. Pigmentation on urostyle and hypural area usually increases somewhat. External dorsal pigmentation on head slowly increases, spreading forward onto snout after about 13 mm. Melanophores form on upper jaw by about 10 mm. In early juveniles, melanophores over mid- and hindbrain spread ventolaterally, reaching level of pectoral-fin origin by about 36 mm. External melanophores present on central opercular area by about 8 mm (Fig. 2C), form indistinct bar across cheek by about 12–15 mm (Fig. 3A). Barbels initially unpigmented, become densely pigmented distally, usually beginning between 6 and 7 mm. As barbels broaden, melanophores become more concentrated along distal margins and after barbel fusion, connecting membrane becomes intensely pigmented along distal margin (by 12–13 mm:

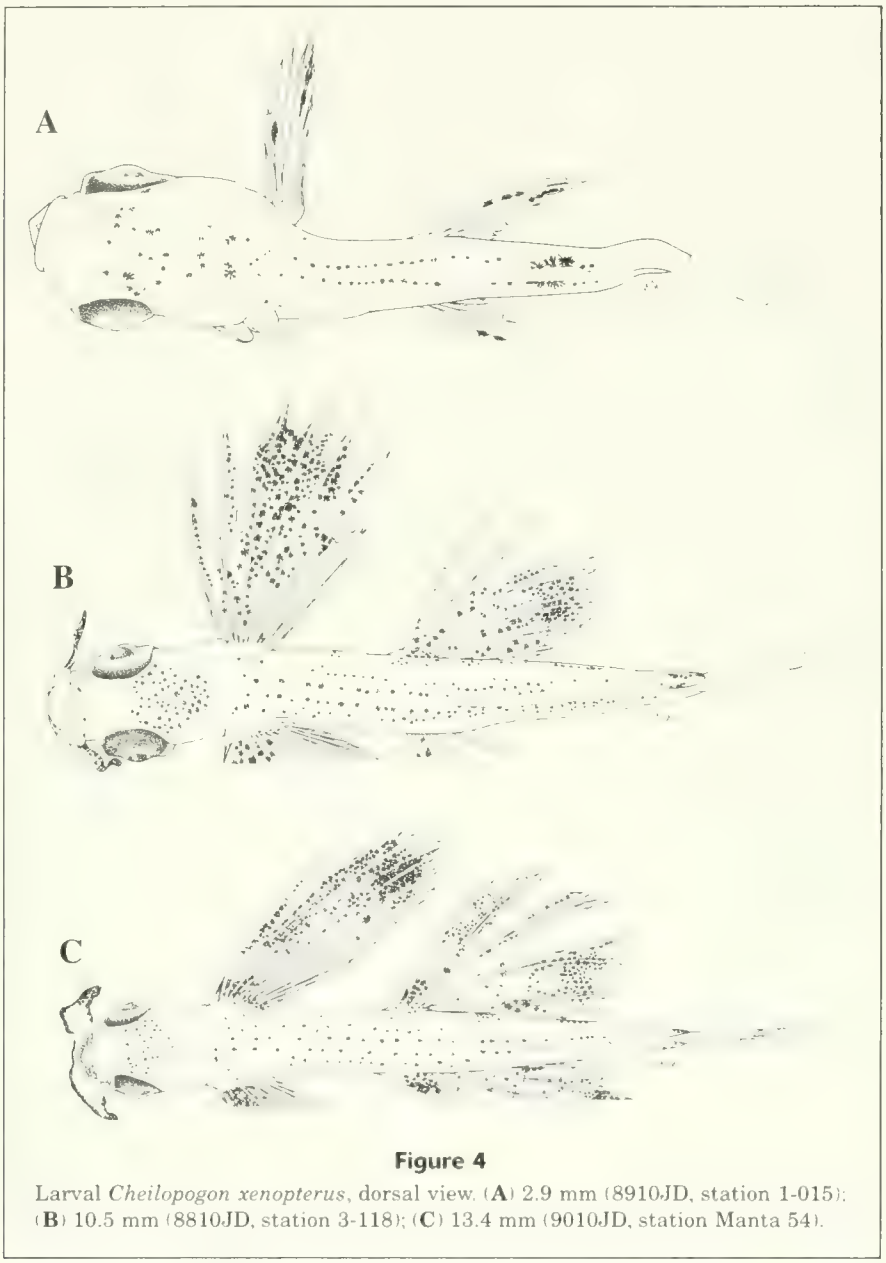

Figure 4

Larval *Cheilopogon xenopterus*, dorsal view. (**A**) 2.9 mm (8910JD, station 1-015); (**B**) 10.5 mm (8810JD, station 3-118); (**C**) 13.4 mm (9010JD, station Manta 54).

Fig. 4C). Few melanophores usually form along lower jaw after about 7 mm.

Soon after hatching, a row of melanophores forms along horizontal septum, originating just behind midtail and spreading cephalad and caudad (primarily cephalad) along tail (Fig. 2, A and B). Barred pattern begins to develop at about 6 mm as melanophores spread upward from pelvic-fin bases and from ventral margins of last three or four preanal myomeres (Fig. 2B). Two more bars begin to spread upward from vicinity of anal-fin rays 5–8 and from midway between pectoral- and pelvic-fin bases (Figs. 2C, 3A) between about 8 and 9 mm. Bars usually do not reach dorsal margin in larvae. Pigmentation on pectoral-fin base sparse until about 8 mm then increases, spreads onto adjacent myomeres, and in juveniles merges with melanophores spreading downward from dorsum to form saddle (Figs. 2C; 3, A and B). Melanophore cluster on hypural area expands to cover almost entire area by about 13 mm. Juveniles thus display six or seven bars (including pectoral saddle); in juveniles >30–40 mm posterior three or four bars most prominent (Fig. 3B).

Pectoral-fin pigmentation initially sparse. After hatching, melanophores gradually spread over membranes between upper 5–6 rays, a few scattered between all but lowermost 3–4 rays, by about 8 mm (Fig. 2, A–C). Pigment patterns variable in larvae

<10–12 mm, except that melanophores tend to be more concentrated near distal margin between upper 5–7 rays and in patch about midway along upper rays. After about 12 mm concentration midway along upper rays commonly persists, but may diminish or disappear, and distal patch expands to form distinct blotch along upper 6–8 rays, bordered by unpigmented (or sparsely pigmented) margin (Fig. 4C). Distal blotch expands into elongate oval band over much of width of pectoral fin in juveniles (Fig. 3B). Upper 4–6 pectoral rays also may remain sparsely to moderately pigmented, especially proximally and in the blotch midway along upper rays, in larger larvae and juveniles. Apart from upper rays and distal blotch or band, remainder of fin has little pigment after ca. 15 mm.

Pelvic-fin pigment may form before hatching; always present after hatching. Sparse initially, commonly sparse to moderate throughout larval development (Fig. 4). Pattern variable: melanophores tend to be more concentrated near distal margin of most or all of fin, in distal patch at innermost ray or between two or three middle rays, or in two distal patches at innermost and outermost rays. Occasionally melanophores more concentrated distally and midway along rays. Distal patch near middle of fin is most common pattern in larger larvae and juveniles.

Caudal-fin pigmentation forms in late embryos, initially proximally, mostly or entirely on lower rays. Pigment increases and spreads to about three-quarters of length of lower principal rays by ca. 8 mm. Melanophores consistently present on upper part of fin by about 8 mm but pigment here is sparse in larvae and sparse to moderate in juveniles.

Diagonal band forms on dorsal fin, originating distally between anterior 2–3 rays just after 8 mm (Fig. 2C) and reaching base of rays 6–7 between 18 and 22 mm. Pigmentation may be sparse in lower (=posterior) part of band and in larger juveniles band appears more like elongate oval patch along first 5–6 rays. Distal blotch forms at last 2–3 rays beginning at about 12–13 mm. Melanophores form on membranes between (primarily adjacent to) first 5–6 rays after 18 mm. Anal fin unpigmented in larvae, but distal blotch forms at last 2–3 rays in juveniles (Fig. 3B).

Comparisons

Eggs

Most exocoetids have spherical eggs that are about 1.5–3 mm in diameter, lack oil globules, and have filaments on the chorion (Collette et al., 1984). *Cheilopogon* eggs are typical exocoetids in these characters. For most of the *Cheilopogon* species the filaments are evenly distributed as in *C. xenopterus*. Only *C. heterurus* and *C. unicolor* have been described as having a different arrangement, with filaments grouped in bipolar clusters (Barnhart, 1932; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Watson, 1996). Among the species with uniform filament distribution, the number of filaments ranges from about 10 to 90; the range in *C. xenopterus* (about 40–60) apparently is typical (e.g. Collette et al., 1984). Filament length in these species ranges from less than 1 mm to just over 10 mm; most commonly the filaments are long, a character shared with *Cypselurus* (e.g. Collette et al., 1984). The short filaments of *Cheilopogon xenopterus* (about 1 mm) are a character shared with *Prognichthys* (Kovalevskaya, 1982) and with at least some of the members of the *C. nigricans* species group (Parin and Belyanina, 1996), which includes *C. dorsomaculata* and *C. xenopterus* in the eastern tropical Pacific. Eggs have not been described for *C. dorsomaculata* or the two *Prognichthys* species in the eastern tropical Pacific (Parin, 1995) and it is unknown how they might be distinguished from the eggs of *C. xenopterus* except that late stage *Prognichthys* embryos should be more densely pigmented. An unidentified type of exocoetid egg (2.2 mm diameter with ca. 150 short filaments) occasionally co-occurs with *C. xenopterus* in plankton samples; it might be one of these species (larval *Prognichthys* are relatively common in the samples).

Collette et al. (1984) noted that some flyingfishes apparently have a preanal finfold during early development and suggested that it is an embryonic feature that is lost soon after hatching. There is no preanal finfold in *C. xenopterus*.

Larvae and juveniles

Larval *Cheilopogon* range between about 4 and 6 mm (e.g. Collette et al., 1984) and are well developed at hatching. *Cheilopogon xenopterus* may be a bit smaller than usual, but otherwise is typical of the genus at hatching. *Cheilopogon* larvae develop a pair of mandibular barbels that persist into the juvenile stage and remain separate or fuse mesially—the membrane joining the barbels either remaining low and simple or becoming broad and fimbriate. Among the *Cheilopogon* species in the eastern Pacific, *C. furcatus*, *C. heterurus hubbsi*, and *C. papilio* retain separate barbels in the juvenile stage. The barbels become fused basally by means of a low, sparsely pigmented or unpigmented membrane in *C. atrisignis* and *C. spilonotopterus*, whereas in *C. dorsomaculata* and *C. xenopterus* the basal membrane is somewhat broader and densely pigmented along its margin.

Only one species, *C. pinnatibarbatus*, is known to have a broad, fimbriate membrane that unites the barbels (Hubbs and Kampa, 1946; Imai, 1959). The barbels become moderately long (Bbl > HL) in *C. atrisignis* and *C. spilonotopterus*, whereas the other species retain relatively short barbels (Bbl < HL). The size and condition of the barbels in *C. rapanouiensis* are unknown, but in the closely related species *C. agoo* they are short (Chen, 1987, 1988).

Larval pigmentation in *Cheilopogon* initially ranges from sparse to dense and typically increases gradually during development. The sparsely pigmented larvae, including *C. xenopterus*, probably *C. atrisignis* and *C. dorsomaculata*, and possibly *C. spilonotopterus* and *C. papilio*, display a pattern primarily of melanophore rows on the dorsum, on the horizontal septum, and on the ventral margin of the tail, and usually bars form in the latter part of the larval stage (Kovalevskaya, 1965, 1977; Chen, 1987, 1988). The more heavily pigmented species, including *C. furcatus*, *C. heterurus hubbsi*, and *C. pinnatibarbatus californicus*, display a pattern similar to that of larval *Cypselurus*, with melanophores more evenly distributed over the trunk and at least anteriorly on the tail (sometimes diminishing to dorsal, midlateral, and ventral rows on the posterior half of the tail) (Hildebrand and Cable, 1930; Hubbs and Kampa, 1946; Watson, 1996). *Cheilopogon rapanouiensis* might belong to this latter group as well, if its larvae resemble the moderately pigmented larvae of *C. agoo* (Chen, 1987, 1988). Juveniles of most species are barred; about six bars (as in *C. xenopterus*) is common.

Larvae and juveniles of *C. xenopterus* usually can be distinguished without great difficulty from the other flyingfish species in the eastern Pacific, except perhaps from *C. dorsomaculata*. The position of the anal-fin origin below dorsal rays 4–7 distinguishes *C. xenopterus* from *Exocoetus*, *Fodiator*, *Hirundichthys*, and *Oxyporhamphus*, in which the anal-fin origin ranges from just ahead of the dorsal-fin origin to under dorsal rays 1–3, depending on species (e.g. Imai, 1954; Kovalevskaya, 1964, 1980; Chen, 1988; Watson, 1996). Larger larvae and juveniles of all four genera are further distinguished from *C. xenopterus* (and all the other *Cheilopogon* species) by their lack of paired mandibular barbels. *Cheilopogon xenopterus* (and all the other flyingfishes) are also distinguished from *Exocoetus* by having much more posteriorly placed pelvic fins. Larval *Fodiator* and *Oxyporhamphus* are unique in developing a beak beginning at about 6 mm and 8 mm, respectively, whereas *Parexocoetus* acquires a much smaller beak in the juvenile stage, by about 18 mm (e.g. Collette et al., 1984; Watson, 1996). *Cheilopogon xenopterus* is rather sparsely pigmented, in contrast to the more general, denser pigmentation of larval *Cypselurus*, *Exocoetus*, *Fodiator*, *Parexocoetus*, *Prognichthys*, and the three or four *Cheilopogon* species noted above (e.g., Hildebrand and Cable, 1930; Imai, 1959, 1960; Kovalevskaya, 1980; Chen, 1988; Watson, 1996). Among the more sparsely pigmented flyingfish larvae, *Hirundichthys* (which may be moderately pigmented initially, but become more sparsely pigmented on at least the prepelvic part of the trunk; e.g. Kovalevskaya, 1980) and *Oxyporhamphus* are easily distinguished from *C. xenopterus* by the characters noted above. In addition, larval *Oxyporhamphus* are more elongate, with much shorter pectoral and pelvic fins, and they lack a row of melanophores along the horizontal septum before about 9 mm (e.g. Khrapkova-Kovalevskaya, 1963; Watson, 1996) in contrast to before 4 mm in *C. xenopterus*. Among the five *Cheilopogon* species in the eastern Pacific with sparsely pigmented (or assumed to be sparsely pigmented) larvae, it usually should be possible to distinguish *C. atrisignis* and *C. papilio* from *C. xenopterus* by a combination of myomere and dorsal, anal, and (in larger larvae) pectoral-fin ray counts (e.g. Table 1). At larger sizes (small larvae have not been described) larval *C. atrisignis* and *C. spilonotopterus* can be distinguished from *C. xenopterus* by barbel structure and pigmentation, and *C. papilio* can be distinguished by barbel structure and fin pigmentation, as noted above. Large larval and juvenile *C. spilonotopterus* are more fully and evenly pigmented on the trunk (by about 14 mm) and lack the barred pattern displayed by larger larval and juvenile *C. xenopterus* (e.g. Kovalevskaya, 1977; Chen, 1987, 1988). *Cheilopogon papilio* likewise become more generally pigmented than *C. xenopterus*, although four or five bars remain visible through at least 21 mm. Juvenile *C. dorsomaculata* smaller than about 40 mm bear a striking resemblance to *C. xenopterus* but can be distinguished by small differences in meristic characters (Table 1) and have more sparsely pigmented (nearly unpigmented) pelvic fins than do *C. xenopterus*. Larvae of *C. dorsomaculata* have not been described, but the similarity of the small juveniles to *C. xenopterus* suggests that it may be difficult to distinguish the larvae of the two species.

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Estimating the harvest of Pacific walrus, *Odobenus rosmarus divergens*, in Alaska

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For thousands of years, walrus hunting has been an important component of the economy and culture of Native communities along the Bering and Chukchi Sea coasts (Ray, 1975). Today, the Pacific walrus (*Odobenus rosmarus divergens*) remains a valuable resource to coastal natives in Alaska (United States) and Chukotka (Russia) as a source of food and raw materials for traditional equipment and handicrafts.

Accurate information regarding the number of animals removed annually from the population is fundamental for the conservation and management of any species. As the agency responsible for managing Pacific walrus in U.S. waters, the U.S. Fish and Wildlife Service (FWS) gathers data on the size and composition of the subsistence walrus harvest in Alaska. The FWS presently administers two separate harvest monitoring programs: the Walrus Harvest Monitoring Project (WHMP) and the Marking Tagging and Reporting Program (MTRP).

The WHMP is an observer program carried out at select walrus hunting villages in Alaska. Each spring, as the pack ice recedes northward, hunters from coastal communities in the Bering Strait region have access to herds of walrus as they migrate to their summer range. Historical harvest information indicates that approximately 80% of the annual reported walrus harvest in Alaska occurs in this region (Fay and Bowlby[1]). WHMP monitors stationed at the primary walrus hunting villages in the Bering Strait region (Gambell, Savoonga, Little Diomede and Wales; Fig. 1) collect information on the size and composition of the walrus harvest. Harvest monitors meet boats as they return from walrus hunting trips in order to collect biological samples and harvest information at the boat landing site (Garlich-Miller[2]). The goal of the WHMP is to identify and record the gender and age class of every walrus retrieved by hunters from these villages during the monitoring period. Although there is no way of evaluating the degree to which this goal is achieved, WHMP monitors meet most of the returning boats, and the number of retrieved animals not recorded during the harvest monitoring period is believed to be small (Dickerson[3]).

The MTRP is a Federally mandated year-round, statewide program (Fig. 1). The marking and tagging rule requires that all hunters certify (tag) walrus ivory (tusks) and report all walruses that are taken. The objectives of the MTRP are to collect harvest information and to certify specified marine mammal parts to help control illegal harvests and trade. Hunters are required to bring walrus tusks to a MTRP tagger within 30 days of the kill. The tagger attaches individually numbered wire tags to the tusks and records the numbers on a tagging certificate. MTRP tags are not attached to calf walruses (or other walruses that may be missing tusks); however, hunters are required to report all animals taken. The age class, gender, kill date, and kill location of each walrus are recorded on the certificate (Stephensen et al.[4]).

These two programs independently provide information on the size and composition of the harvest. Except in the case of the village of Wales, WHMP and MTRP staff are different people. Each of the two monitoring programs has its strengths and weaknesses. The WHMP benefits from the presence of on-site staff to collect accurate biological information from every walrus retrieved in a community during the monitoring period. Unfortunately, the monitoring period is seasonal (restricted to the spring hunt) and operates only in four coastal villages. The MTRP is a statewide, year-round program; however hunter compliance with the MTRP rule is variable and animals lacking tusks (e.g. calves, yearlings, and animals with broken tusks) often go unreported (Burn, 1998).

[1] Fay, F. H., and C. E. Bowlby. 1994. The harvest of Pacific walrus, 1931–1989. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. Technical report MMM 94-2,43 p.

[2] Garlich-Miller, J. 1997. Age, sex, and reproductive status of Pacific walrus harvested in the Bering Strait region, 1994–1996. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. Technical Report MMM 97-1,25 p.

[3] Dickerson, L. 1989. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. Personal commun.

[4] Stephensen, W. D., D. Cramer, and D. Burn. 1994. Review of the Marine Mammal Marking Tagging and Reporting Program, 1982–1992. U.S. Fish and Wildlife Service, Marine Mammals Management, Anchorage, AK. Technical Report MMM 94-1, 49 p.

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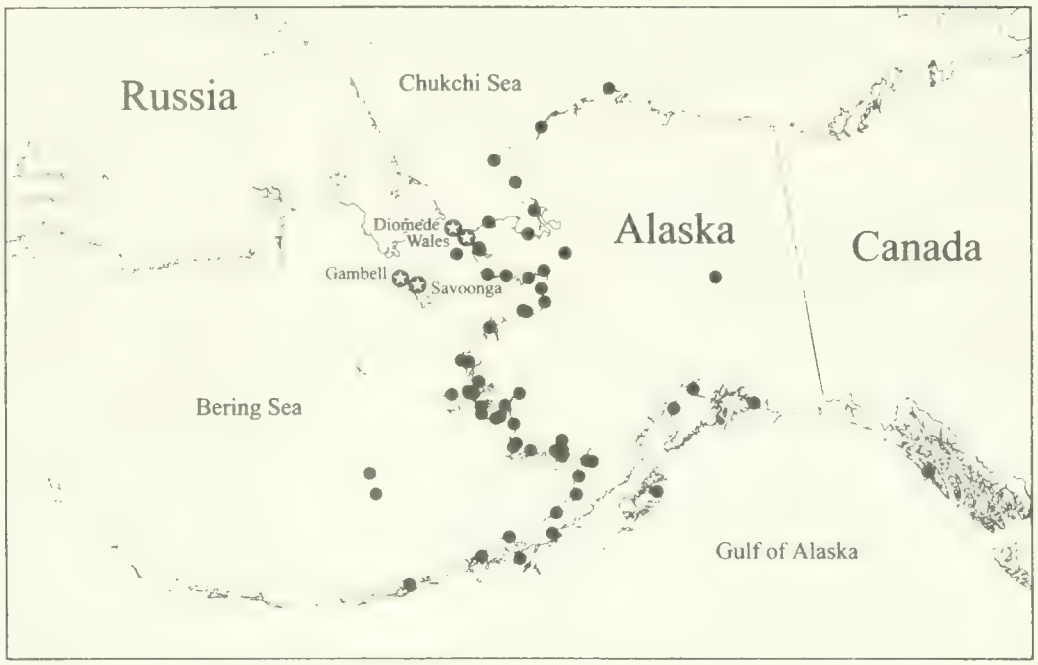

Figure 1

Location of Alaska villages where walrus harvest information is collected through the Walrus Harvest Monitor Project (✪) and the Marking Tagging and Reporting Program (●). Note that tusks may be tagged in selected locations outside the walrus' range.

Owing to funding and logistical constraints that prevent the year-round, statewide implementation of the WHMP and imperfect hunter compliance with the MTRP, not all harvested walruses are recorded. The FWS must therefore rely on analytical methods to estimate the size of the total annual harvest based on the best available information. Here we describe a new method for estimating the size of the annual walrus harvest in Alaska using a correction factor for noncompliance with the MTRP rule.

Materials and methods

Prior to the initiation of the MTRP, the statewide walrus harvest was approximated by using a prediction equation applied to WHMP data. The prediction equation was based upon the historic relationship of the size of the spring harvest at WHMP-monitored villages in relation to the remaining hunting villages in Alaska. This information was obtained from the Alaska Department of Fish and Game, which administered a statewide harvest monitoring program between the years of 1960 and 1978. To estimate the statewide harvest, the FWS used a least-squares regression to describe the relation between the Gambell, Savoonga, and Diomede harvests to the statewide totals. The resulting prediction equation (Equation 1, r^2=0.239) was subsequently used to estimate the total statewide harvest on the basis of data collected annually after 1978 through the WHMP at Gambell, Savoonga, and Diomede.

$$N = 459.7 + 1.26\,(WHMP_{Total}), \qquad (2)$$

where N = total statewide harvest estimate; and
$WHMP_{Total}$ = total number of retrieved walruses recorded during monitored spring hunts at select villages (Diomede, Gambell, and Savoonga) for a given year.

The evolution of the MTRP as a year-round, statewide monitoring program provided the opportunity to improve the reliability of harvest estimates by using current data. Because there is spatial and temporal overlap between the two programs, the WHMP can serve as a baseline for evaluating compliance with the MTRP program. A correction factor for noncompliance can be estimated as a proportion by using the following equation:

$$R = \frac{WHMP_{Total}}{MTRP_{WHMP}}, \qquad (2)$$

Table 1

Walrus harvest data from the Walrus Harvest Monitor Project (WHMP) and Marking, Tagging, and Reporting Program (MTRP), 1992–1997.

Year	$WHMP_{Total}$	$MTRP_{WHMP}$	Correction factor (R)	Standard error SE(R)	$MTRP_{Total}$	Prediction Equation 1	Proportional Equation 3	95% CI of Equation 3
1992	820	976			1700	1491[1]		
1993	710	708	1.003	0.21	1189	1353	1192	703–1682
1994	971	799	1.215	0.17	1328	1681	1614	1171–2056
1995	1204	785	1.534	0.17	1096	1974	1681	1316–2046
1996	1220	773	1.578	0.33	1572	1994	2481	1464–3497
1997	856	574	1.491	0.09	1045	1537	1558	1373–1742

[1] The calculated estimate was less than the value of $MTRP_{Total}$. The $MTRP_{Total}$ was therefore used as a minimum estimate of the statewide walrus harvest.

where R = correction factor for noncompliance; and

$MTRP_{WHMP}$ = a subset of the number of walruses recorded through the MTRP with reported kill dates and locations that coincide with WHMP operations (presumed to have been recorded through both the MTRP and the WHMP).

The standard error of this ratio estimate is calculated according to Snedecor and Cochran (1967, p. 537) by treating each of the three villages as independent estimates of overall compliance. Data from the village of Wales were not used in the analysis because of small harvests and a lack of independence between the WHMP and MTRP programs in that village.

Assuming the estimated compliance with the MTRP is uniform throughout the full range of walrus hunting villages, the total MTRP harvest can be adjusted as follows:

$$N = MTRP_{Total} \times R, \quad (3)$$

where $MTRP_{Total}$ = the total number of walrus recorded through the MTRP.

Results

Data from the MTRP and WHMP are currently available for the years 1992–97 (Table 1). Estimated compliance with the MTRP (the reciprocal of R) ranged from 63% to 99%. Harvest estimates based on the prediction equation and the proportional equation differed depending on the proportion of animals recorded through each of the two monitoring programs. The difference between the two methods was not statistically significant for any year. Comparisons of the 1992 MTRP and WHMP harvest data suggests that the WHMP monitors were unable to account for all the retrieved walruses landed during the monitoring period. In this instance, the $MTRP_{Total}$ was considered the minimum estimate of the statewide harvest.

Discussion

Prior to 1997, the FWS used WHMP data collected annually at Gambell, Savoonga, and Diomede as an index for estimating the total statewide harvest of walrus. One drawback of this method has been that the equation assumes that the relation between the hunting success of WHMP and non-WHMP villages is constant over time (Fay et al., 1997). In fact, recent harvest data have shown that the relative hunting success of each village is highly variable. The annual harvest at each village is subject to large interannual variation, presumably as a result of weather and ice patterns affecting the availability of walruses to hunters at a given geographical location (Garlich-Miller[2]).

One advantage of the proportional equation (Eq. 3) over the prediction equation (Eq. 1) is that it can account for variability in the relative success of hunting villages. For example, on the basis of comparable numbers of walrus recorded through the WHMP in Gambell, Savoonga, and Diomede in 1995 and 1996, the prediction equation produced remarkably similar harvest estimates for the two years (1974 and 1994 walrus, respectively). Although MTRP compliance rates were also comparable for these years, the proportional equation, in which statewide MTRP data were used, produced harvest estimates that were markedly different (1681 and 2481 walrus, respectively). We

believe that this difference, which reflects interannual variability in the hunting success of non-WHMP villages, more accurately reflects statewide harvest levels for these two years. For the reasons stated above, the FWS has adopted the use of the proportional equation to estimate the size of the walrus harvest.

In 1992, the assumption that all retrieved walrus were recorded during WHMP operations was not met. In this instance we considered the uncorrected MTRP data as a minimum harvest estimate for that year. The WHMP was re-initiated in 1992 after a two-year hiatus; the lack of experienced personnel likely contributed to the poor monitoring results that season. Since that time, program managers have attempted to improve the program by hiring experienced monitors and additional village assistants to meet all returning boats and by emphasizing the importance of recording all retrieved animals (Dickerson[3]).

Another assumption of the proportional equation is that compliance in the villages of Gambell, Savoonga, and Diomede is representative of non-WHMP villages. Compliance was variable between villages and years, suggesting that there was little correlation between the two programs. Since conducting analyses of MTRP compliance, information and education efforts in these villages appear to have been effective at increasing compliance. The accuracy of this method could be improved by increasing the number of villages in the WHMP.

In both the prediction and proportional equations, estimates are based on the number of walrus that are retrieved by hunters. Fay et al. (1994) estimated that 42% of walrus struck by hunters are not retrieved and subsequently die at sea. In order to estimate total human-caused removals from the Pacific walrus population, harvest estimates are adjusted to account for animals struck and lost.

Accurate harvest data are vital to the management of the Pacific walrus population. Harvest data are incorporated into stock assessment reports that chart the status and trend of the population. The stock assessment process compares estimates of human-caused mortality with a calculated potential biological removal (PBR) level to determine the status of a stock. One of the reasons a stock may be designated as "strategic" depends upon whether or not its level of human-caused mortality exceeds the calculated PBR level (Wade, 1998). Since 1992, most human caused mortality affecting the Pacific walrus population has been associated with walrus hunting activities in Alaska and Chukotka. Between 1992 and 1996 the combined annual take of walrus in the U.S. and Russia averaged 4869 walrus per year (Gorbics et al.[5]). Russian harvest data are currently unavailable for 1997. Because annual estimates of human caused mortality have been lower than the calculated PBR of 7533 the population has been classified as non-strategic (Gorbics et al.[5]). It is essential that harvest monitoring in both nations be maintained in order to accurately assess the impact of the harvest to this stock.

In summary, this new method of harvest estimation uses data from both harvest monitoring programs to account for interannual and intervillage variability in hunting success and applies a correction factor to adjust total harvest estimate to account for noncompliance with the MTRP. The accuracy of harvest estimates is therefore dependent upon the degree of hunter compliance with the MTRP rule. It is hoped that through ongoing information and education efforts that explain the importance of accurate harvest data, the understanding of and compliance with monitoring programs will improve.

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The trophic role of Atka mackerel, *Pleurogrammus monopterygius*, in the Aleutian Islands area

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Atka mackerel (*Pleurogrammus monopterygius*) is presently the most abundant marine fish species in the Aleutian Islands. Its exploitable biomass in 1998 was estimated to be 535,500 metric tons (t) (Lowe and Fritz[1]). The commercial catch of Atka mackerel increased from 26,740 t in 1991 to 104,000 t in 1996 (Lowe and Fritz[1]). Atka mackerel has been identified as food for other marine fishes, i.e. Pacific cod (*Gadus macrocephalus*) (Andriyashev, 1937), coho salmon (*Oncorhynchus kisutch*) (Wing, 1985; Volkov et al., 1995; Davis[2]), arrowtooth flounder (*Atheresthes stomias*) (Mito, 1974); sea birds such as thick-billed murres (*Uria lomvia*) (Ogi, 1980); and marine mammals such as Steller sea lions (*Eumetopias jubatus*) (Merrick et al., 1997). The western stock of Steller sea lions has recently been listed as endangered. A connection between the observed decline in Steller sea lions and the sea lion's dependence on commercially exploited fish species such as Atka mackerel as prey has been suggested (Merrick et al., 1997). Because of the great abundance of Atka mackerel and its important role as food for marine fish and marine mammals, it is essential to understand the trophic role of Atka mackerel in the Aleutian Islands area. The objective of this study was to describe the role of Atka mackerel as prey and as predator in the Aleutian Islands ecosystem.

Methods

Study area

From July to September 1991, the Resource Assessment and Conservation Engineering (RACE) Division at the Alaska Fisheries Science Center (AFSC), Seattle, Washington, conducted a groundfish resources trawl survey in the Aleutian Islands region. This area (Fig. 1) was divided into four major geographical units: southeastern Bering Sea area (from long. 165°W to 170°W, 42,604 km^2); eastern Aleutian area (long. 170°W to 177°W, 338,818 km^2); central Aleutian area (long. 177°W to 177°E, 322,234 km^2); and western Aleutian area (long. 177°E to 170°E, an area of 343,083 km^2). Two chartered fishing vessels, *Ocean Hope* and *Green Hope*, were used. Both vessels used standard RACE Division Poly-Nor'eastern, hard bottom, high-opening bottom trawls constructed of 12.7-cm (5-inch) stretched-mesh polyethylene web, with a 3.2-cm (1-1/4 inch) stretched-mesh nylon liner in the codend to retain smaller specimens (Harrison, 1993). Trawls were towed at 3 knots for 30 minutes. Scientists from the Resource Ecology and Fisheries Management (REFM) Division, Resource Ecology and Ecosystem Modeling Task, collected fish stomach samples during this survey.

Sample collection

Fish stomach samples were collected during trawling operations by scientists aboard the charter vessel *Green Hope*. Both Atka mackerel and their potential fish predators were sampled and measured, and stomach samples were collected. Because of the previously demonstrated high similarity (>60%) in diet between arrowtooth flounder and Kamchatka flounder (Yang and Livingston, 1986), no stomach samples of Kamchatka flounder were collected. Before excising a stomach, fish were examined for evidence of regurgitation or net feeding. If a fish had food in its mouth or around the gills, or if its stomach was everted or flaccid, the fish was categorized as having regurgitated food and the specimen was discarded. If a predator had fresh food (usually fish) sticking out of its mouth or throat, it was categorized as a net-feeding fish and was also discarded. When a sampled stomach was retained, it was put into a cloth stomach bag. A field tag with the species name, fork length (FL), and haul data (vessel, cruise, haul number, and specimen number) was also put into the bag. All of the samples collected were then preserved in buckets containing a 10% buffered formalin solution. When

[1] Lowe, S. A., and L.W. Fritz. 1997. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for November 1997, compiled by the plan team for the groundfish fisheries of the Bering Sea and Aleutian Islands. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

[2] Davis, N. D. 1990. U.S.-Japan cooperative high seas salmonid research in 1990: summary of research aboard the Japanese research vessel *Hokuho maru*, 4 June to 19 July. (INPFC Doc. 3508) FRI-UW-9010. Fish. Res. Inst., Univ. Washington, Seattle, WA 98195, 24 p.

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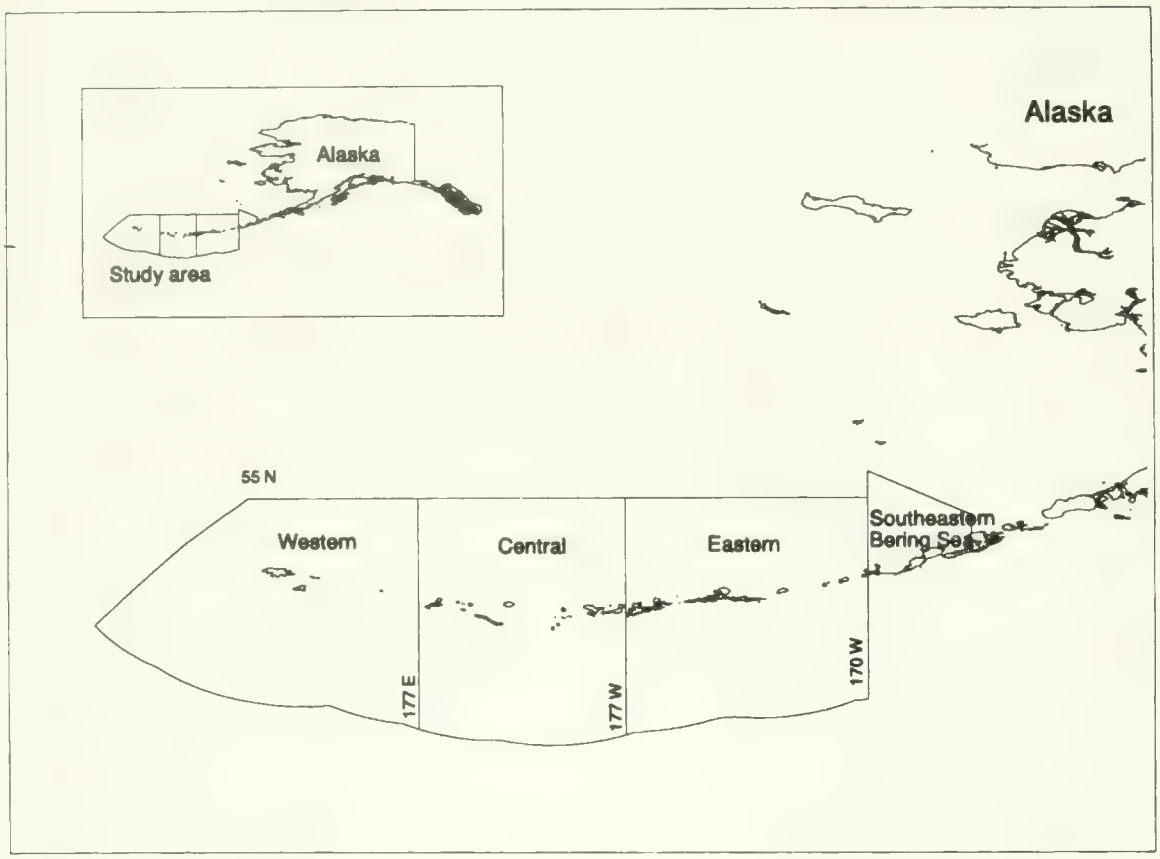

Figure 1
The subareas of the Aleutian Islands trawl survey area.

the samples arrived at the laboratory, they were transferred to 70% ethanol before the contents were analyzed.

Stomach content analysis

In the laboratory, stomach contents were first blotted with a paper towel and the wet weight recorded to the nearest one-tenth of a gram. After obtaining the total weight of the contents, these were placed in a petri dish and examined under a dissecting microscope. Each prey item was classified to the lowest practical taxonomic level. The numbers of noncommercially important prey were not counted; instead the percent total volume of these prey items in stomachs was visually estimated. Prey weights and numbers of commercially important crabs and fish were recorded. If walleye pollock otoliths were found, otolith lengths were measured and the pollock's standard length (SL) was derived through an otolith length-fish length regression table (from REFM's Ageing Task). Other fish otoliths were not treated as walleye pollock otoliths either because they were not found as frequently as walleye pollock or were difficult to identify to the species level. Standard lengths of prey fish, carapace widths (CW) of Tanner crabs (*Chionoecetes* spp.), and Korean horse-hair crabs (*Erimacrus isenbeckii*) were also recorded.

Data analysis

Atka mackerel as prey and predator The general diet of each species was analyzed to determine the overall percent total weight that each prey item represented in the stomach and to identify predators of Atka mackerel. Marine fishes that were mainly fish eaters were then selected for an analysis of population consumption of Atka mackerel. Stomach content analysis of Atka mackerel were performed to understand the role of Atka mackerel as a predator in the Aleutian Islands area.

Population level consumption of Atka mackerel by marine fish Following their identification as predators, the consumption of Atka mackerel by four marine fish species, Pacific cod, Pacific halibut, arrowtooth flounder, and Kamchatka flounder, was estimated. The amount of Atka mackerel consumed

at the population level was calculated by using the following equation:

$$\sum C_i = DR_i \times D \times B_i \times P_i,$$

where C_i = the consumption (by weight) of Atka mackerel by size group i of a predator species;

DR_i = the daily ration (as a proportion of body weight per day) of predator size group i (Table 1);

D = the number of days when Atka mackerel were vulnerable to predation (from 1 May to 30 September in this study);

B_i = the biomass of the predator size group i (Table 2); and

P_i = the proportion by weight of prey Atka mackerel in the diet of predator size group i (Table 3).

Daily rations were calculated by using annual growth increments and conversion efficiencies (Brett and Groves, 1979). Predator biomass data were obtained from the RACE Division database at the AFSC. The percent by weight of prey Atka mackerel in the diet of predators (P_i) was calculated for arrowtooth flounder, Pacific cod, and Pacific halibut. Because of the high similarity (>60%) between the diets of Kamchatka flounder and arrowtooth flounder (Yang and Livingston, 1986), the percent by weight of Atka mackerel that arrowtooth flounder consumed was also used for Kamchatka flounder.

Results

Atka mackerel as prey of marine fishes

Eleven commercially important groundfish species were collected: Pacific cod, *Gadus macrocephalus*; walleye pollock, *Theragra chalcogramma*; Pacific halibut, *Hippoglossus stenolepis*; arrowtooth flounder, *Atheresthes stomias*; Greenland turbot, *Reinhardtius hippoglossoides*; Atka mackerel, *Pleurogrammus monopterygius*; Pacific ocean perch, *Sebastes alutus*; northern rockfish, *S. aleutianus*; shortraker rockfish, *S. borealis*; and shortspine thornyhead, *Sebastolobus alascanus*. According to stomach content data, Atka mackerel (mostly juveniles) were found in the stomachs of Pacific cod, Pacific halibut, and arrowtooth flounder. The detailed food habits of these species were previously reported (Yang, 1996). The mean percent weights of Atka mackerel consumed by the predators are given in Table 3 by predator size and subarea. Arrowtooth flounder >40 cm FL consumed large amounts (36.6% by weight) of Atka mackerel in the western Aleutian area, whereas Pacific cod >60 cm FL and Pacific halibut (especially fish >80 cm FL) both consumed great amounts of Atka mackerel in the central Aleutian area (42% and 72.9% by weight, respectively).

Table 1

Daily ration (DR_i, in terms of proportion of body weight per day) of four groundfish predators in the Aleutian Islands area in 1991.

Predator species	Predator size (cm)	Daily ration
Arrowtooth flounder and Kamchatka flounder	<20	0.009
	20–39	0.005
	≥40	0.008
Pacific cod	<30	0.011
	30–59	0.011
	≥60	0.008
Pacific halibut	50–79	0.004
	≥80	0.007

Atka mackerel as predator

A total of 238 Atka mackerel stomachs were analyzed, 231 (97%) of which contained food. Atka mackerel ranged from 22 to 44 cm FL, with a mean and SD of 33.5 cm and ±4.5 cm, respectively. Table 4 lists the percent by weight of the prey found in Atka mackerel stomachs. More than 90% of the total weight of stomach contents was invertebrates and less than 5% was fish. Euphausiids (mainly *Thysanoessa inermis*) were the most important prey, representing more than 28% of the total stomach contents. Calanoid copepods were another important prey of Atka mackerel, representing approximately 23% of the total stomach content weight. Larvaceans and *Themisto* sp., a hyperiid amphipod, occurred frequently but each represented less than 10% of the total weight of stomach contents. Squid were another invertebrate prey of Atka mackerel; they represented 5% of the total weight of stomach contents.

Several fish species were preyed on by Atka mackerel. Walleye pollock represented 2.4% by weight of the total stomach contents. Myctophids, bathylagids, zoarcids, stichaeids, and pleuronectids were also found. However, each of them represented less than 1% of the total weight of stomach contents. Cannibalism of eggs was also observed in Atka mackerel stomachs, and eggs represented 5.5% of the total weight of stomach contents.

Figure 2 shows the percentage by weight of the main prey items for different Atka mackerel size

Table 2

Biomass (B_i ; in tons) of predators of Atka mackerel by size groups in three subareas (W, C, E) around the Aleutian Islands and southeastern Bering Sea (SBS) in 1991. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; ATKA = Atka mackerel; KF = Kamchatka flounder; W = western Aleutian; C = central Aleutian; E =eastern Aleutian.

Species (cm)	W	C	E	SBS	Total
ATF					
<20	1.9	0.6	29.4	37.6	
20–39	947.8	728.1	2162.1	4276.3	
≥40	3796.2	1571.1	4733.5	8315.8	
Total	4745.9	2299.8	6925.0	12,629.8	26,601
PCOD					
<30	12.5	153.7	138.6	151.6	
30–59	5507.2	9791.5	15,010.9	3886.2	
≥60	57,847.8	28,355.0	46,159.4	7448.3	
Total	63,367.6	38,300.2	61,308.8	11,486.1	174,463
PH					
<50	0	157.5	204.5	1857.8	
50–79	560.1	1795.1	6813.4	2891.8	
≥80	4745.9	5267.2	11,123.4	4207.9	
Total	5306.0	7219.8	18,141.3	8957.7	39,625
ATKA					
≤25	2537.9	2267.6	2000.0	0	
26–35	142,607.1	86,328.5	65,407.6	0	
>35	175,047.2	185,358.4	2629.7	0	
Total	320,192.3	273,954.5	70,037.4	0	664,184
KF					
<20	0	0	9.3	0	
20–39	280.9	251	442.2	4.8	
≥40	5281.5	9028.7	1114.6	881.7	
Total	5562.4	9279.7	1566.1	886.6	17,295

Table 3

Mean percent weight (P_i) of Atka mackerel consumed by marine fish in three subareas (W, C, E) around the Aleutian Islands and southeastern Bering Sea (SBS) in 1991. (—) indicates no sample. Values in parentheses are sample sizes. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut. W = western Aleutian; C = central Aleutian; E = eastern Aleutian.

Species (cm)		W	C	E	SBS
ATF	<20	—	—	0 (1)	0 (6)
	20–39	0 (20)	0 (9)	0 (56)	0 (36)
	>40	36.6 (19)	0 (3)	0 (28)	14.3 (16)
	Total	32.1 (39)	0 (12)	0 (85)	7.1 (58)
PCOD	<30			0 (3)	0 (31)
	30–59	5.0 (78)	14.5 (44)	0 (68)	0 (28)
	>60	25.3 (117)	41.7 (23)	5.6 (145)	0 (14)
	Total	24.1 (195)	40.2 (67)	3.6 (316)	0 (73)
PH	[illegible]	[illegible]	[illegible]	0 (5)	0 (47)
	50–79	4.0 (10)	36.0 (7)	0 (39)	9.8 (33)
	[illegible]	[illegible]	[illegible]	0.2 (10)	0 (6)
	Total	28.2 (22)	33.8 (18)	0.1 (54)	4.0 (86)

groups. The most important food of the smallest (≤25 cm) size group of Atka mackerel were calanoid copepods (35% by weight) and larvaceans (33%). The most important prey of Atka mackerel between 26 and 35 cm FL were calanoid copepods (35%) and euphausiids (29%). The largest size group (>35 cm) of Atka mackerel consumed a substantial amount of calanoid copepods (18%), in addition to euphausiids (22%). Miscellaneous fish (walleye pollock, cottids, myctophids, and zoarcids) represented approximately 9% of the total weight of stomach contents of the largest size group of Atka mackerel. Atka mackerel eggs (as evidence of cannibalism) were found almost exclusively in the largest size group, representing 11% of total weight of stomach contents.

Walleye pollock were the most common fish species in the Atka mackerel diet. The size of walleye pollock consumed ranged from 49 to 63 mm SL with a mean and SD of 56.2 mm and ±4.8 mm, respectively. The cottids consumed by Atka mackerel ranged from 12 to 21 mm SL with mean and SD of 15.9 mm and ±3.1 mm, respectively. In addition, Atka mackerel stomach samples contained one bathylagid

Table 4

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the prey items of Atka mackerel (*Pleurogrammus monoptgerygius*) collected in the Aleutian Islands area in 1991.

Prey name	%W	%FO	Prey name	%W	%FO
Polychaeta (worm)	0.62	2.59	Caridea (shrimp unidentified)	0.11	15.45
Gastropoda (snail)	0.88	34.86	Hippolytidae (shrimp)	0	0.48
Pteropoda	0.03	3.89	Pandalidae (shrimp)	0.12	0.32
Cephalopoda (squid and octopus)	0.07	5.29	Paguridae (hermit crab)	0	2.06
Teuthoidea (squid)	4.67	27.26	Majidae (spider crab)	0.06	3.81
Octopoda (octopus)	0.09	1.27	*Hyas* sp. (lyre crab)	0.02	3.66
Crustacea (unidentified)	4.89	6.98	*Chionoecetes* sp. (snow and Tanner crab)	0.06	6.72
Ostracoda (unidentified)	0.04	12.79	*Erimacrus isenbeckii* (Korean horse-hair crab)	0	0.32
Calanoida (copepod unidentified)	22.68	61.12	Cancridae (crab)	0.03	0.32
Eucalanidae (copepod)	0.23	5.49	Ectoprocta (bryozoan)	0.02	1.98
Eucalanus sp. (copepod)	0.01	1.29	Chaetognatha (arrow worm)	0.79	23.71
Pseudocalanus sp. (copepod)	0	0.34	Larvacea Copelata	9.05	72.28
Candacia columbiae (copepod)	0.51	45.00	Chondrichthyes	0.01	1.66
Mysidacea (mysid unidentified)	0.01	1.59	Osteichthyes Teleostei (bony fish unidentified)	0.1	1.27
Mysidacea Mysida (mysid)	0.01	0.63	Bathylagidae (deepsea smelts)	0	0.48
Acanthomysis pseudomacropsis (mysid)	0	0.48	Myctophidae (lanternfish)	0.75	0.95
Cumacea (cumacean unidentified)	0.02	5.29	*Theragra chalcogramma* (walleye pollock)	2.4	2.06
Amphipoda (amphipod unidentified)	0.02	1.82	Zoarcidae (eelpout)	0.67	0.32
Gammaridea (amphipod)	0.84	16.36	Atka mackerel eggs	5.52	6.67
Themisto sp. (amphipod)	2.41	59.16	Stichaeidae (prickleback)	0.01	0.32
Caprellidea (amphipod)	0.02	2.45	Pleuronectidae (flatfish)	0.01	0.32
Euphausiacea (euphausiid unidentified)	27.46	60.08	Unidentified organic material	10.39	28.49
Euphausia sp. (euphausiid)	0.03	0.48	Fishery discards	0.58	0.32
Euphausia pacifica (euphausiid)	0.02	0.48			
Thysanoessa inermis (euphausiid)	0.75	0.48	Total prey weight	700.55 g	
Thysanoessa inspinata (euphausiid)	0.14	0.32	Total nonempty stomachs	231	
Thysanoessa longipes (euphausiid)	0.1	0.48	Total empty stomachs	7	
Thysanoessa spinifera (euphausiid)	0.19	0.95	Total hauls	21	

(11 mm SL), one zoarcid (61.4 mm SL), one myctophid (59 mm SL), and one stichaeid (29 mm SL).

Consumption of Atka mackerel at the population level

The dominant predator species, Pacific cod and Pacific halibut, consumed large amounts of Atka mackerel (Table 5). The estimated amount of Atka mackerel consumed by each species varied by predator size as well as by the location where the predator was collected. For Pacific cod, large fish (≥60 cm) in the western and central Aleutian areas consumed between 14,000 and 18,000 t of Atka mackerel. For Pacific halibut, large fish (≥80 cm) consumed between 2000 and 4000 t in the western and central Aleutian Islands areas. Consumption of Atka mackerel by arrowtooth flounder was found in samples

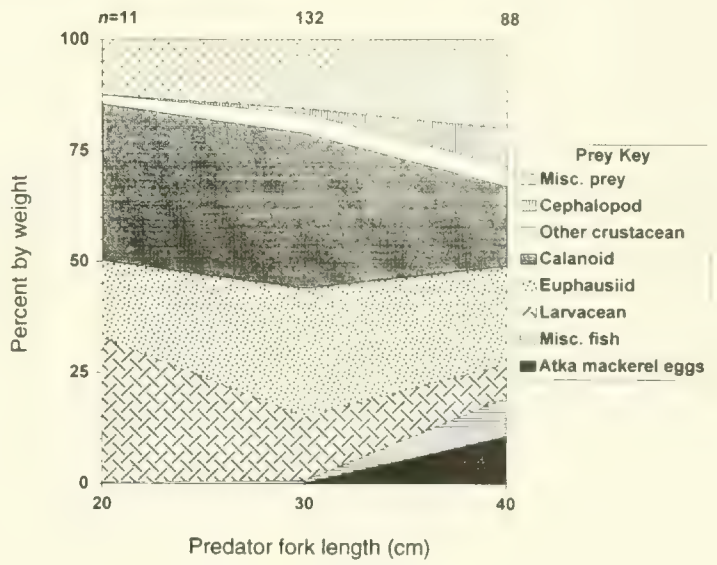

Figure 2

Variation in the main food items of Atka mackerel, by predator size, in the Aleutian Islands area in 1991. *n* = sample size.

Table 5

Biomass (t) of Atka mackerel population consumed by marine fishes in three subareas (W, C, E) around the Aleutian Islands and the southeastern Bering Sea (SBS) area in 1991. (—) indicates no sample. Values in parentheses are % total biomass. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; KF = Kamchatka flounder. W = western Aleutian; C = central Aleutian; E = eastern Aleutian.

Species	(cm)	W	C	E	SBS	Total
ATF	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	>40	1702 (3.5)	0	0	1455 (3.0)	3157 (6.5)
	Total	1702 (3.5)	0	0	1455 (3.0)	3157 (6.5)
PCOD	<30	—	—	0	0	0
	30–59	460 (1.0)	2394 (4.9)	0	0	2854 (5.9)
	≥60	17,914 (36.9)	14,487 (29.9)	3170 (6.5)	0	35,570 (73.3)
	Total	18,374 (37.9)	16,881 (34.8)	3170 (6.5)	0	38,424 (79.2)
PH	<50	0	0	0	0	0
	50–79	14 (0.1)	395 (0.8)	0	173 (0.4)	582 (1.2)
	≥80	1958 (4.0)	4114 (8.5)	19 (0.1)	0	6091 (12.6)
	Total	1972 (4.1)	4509 (9.3)	19 (0.1)	173 (0.4)	6673 (13.8)
KF	<20	—	—	0	0	0
	20-39	0	0	0	0	0
	≥40	126 (0.3)	0	0	154 (0.3)	280 (0.6)
	Total	126 (0.3)	0	0	154 (0.3)	280 (0.6)
	All species	22,173 (45.6)	21,390 (44.1)	3189 (6.6)	1782 (3.7)	48,534

from the western Aleutian and southeastern Bering Sea areas. Because the diet of arrowtooth flounder and Kamchatka flounder are very similar (Yang and Livingston, 1986), the daily ration values (Table 1) and the values of the mean percent of the Atka mackerel consumed by arrowtooth flounder (Table 3) were used for the calculation of the consumption of Atka mackerel by Kamchatka flounder. The total biomass of Atka mackerel consumed by the main marine fishes in the Aleutian Islands areas was 48,534 t (Table 5).

The number of Atka mackerel consumed by marine fishes was also estimated from the biomass consumed (Table 5) and the prey length recorded from stomach content analysis. The total number of Atka mackerel consumed by marine fishes in the Aleutian Islands area was about 284 million (Table 6), 84% of which were consumed by Pacific cod. The size and age composition of Atka mackerel consumed by groundfishes is listed in Table 7. Age-2 fish represented about 40% of the total numbers of Atka mackerel consumed by groundfishes, including predators of all sizes from different areas. Age-1 and age-3 fish accounted for 30% and 22% of the total numbers consumed, respectively. Age-0 Atka mackerel (4%) were consumed only by Pacific cod ≥60 cm FL in the central Aleutian area. Some age-4 and age-6 Atka mackerel were also found in marine fish stomachs, but they accounted for only about 4% of the total number consumed compared with about 25% of the Atka mackerel that were age 3. In terms of biomass, the age 2+ Atka mackerel consumed by marine fishes (41,071 t) represented about 3.2% of the estimated Atka mackerel population biomass (age 2+) (Lowe and Fritz[1]).

Discussion

Atka mackerel as prey of marine fishes

In addition to groundfish, such as Pacific halibut, Pacific cod, arrowtooth flounder, and Kamchatka flounder that feed on Atka mackerel, other marine fishes also consume Atka mackerel. Several authors have reported that pelagic salmonids prey on Atka mackerel. Davis[2] found that coho salmon (*Oncorhynchus kisutch*) ate Atka mackerel in the North Pacific Ocean. Volkov et al. (1995) found that Atka mackerel represented 30% and 13% of the food composition of coho salmon in the Sea of Okhotsk and the western Kamchatka areas, respectively. Gorbunova (1970) stated that 25–30 mm long larvae of Atka mackerel were found frequently in the stomachs of salmon caught in the open sea. In this study, no larval Atka mackerel were found in the stomachs of marine fishes, only juveniles or adults.

Table 6

Numbers (thousand) of Atka mackerel population consumed by marine fishes in three subareas (W, C, E) around the Aleutian Islands and the southeastern Bering Sea (SBS) in 1991. (—) indicates no data. Values in parentheses are % total numbers. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; KF = Kamchatka flounder; W = western; C = central; E = eastern.

Species	(cm)	W	C	E	SBS	Total
ATF	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	>40	7217 (2.5)	0	0	9419 (3.3)	16,639 (5.9)
	Total	7217 (2.5)	0	0	9419 (3.3)	16,636 (5.9)
PCOD	<30	—	—	0	0	0
	30–59	3668 (1.3)	47,081 (16.6)	0	0	50,749 (17.9)
	≥60	75,358 (26.5)	113,249 (39.9)	0	0	188,607 (66.4)
	Total	79,026 (27.8)	160,330 (56.5)	0	0	239,356 (84.3)
PH	<50	0	0	0	0	0
	50–79	0	3390 (1.2)	0	0	3390 (1.2)
	≥80	6856 (2.4)	16,242 (5.7)	0	0	23,098 (8.1)
	Total	6856 (2.4)	19,632 (6.9)	0	0	26,488 (9.3)
KF[1]	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	≥40	534 (0.2)	0	0	999 (0.4)	1533 (0.5)
	Total	534 (0.2)	0	0	999 (0.4)	1533 (0.5)
	All species	93,633 (33.0)	179,962 (63.4)	0	10,418 (3.7)	284,013

[1] I used ATF stomach content data and KF biomass.

Table 7

Numbers (thousand) by age (yr) and size (mm) of Atka mackerel consumed by the marine fishes in the Aleutian Islands area in 1991. ATF = arrowtooth flounder; KF = Kamchatka flounder; PH = Pacific halibut; COD = Pacific cod; w = western Aleutian; c = central Aleutian; sbs = southeastern Bering Sea.

Predator	Age 0 <131	Age 1 131–206	Age 2 207–261	Age 3 262–302	Age 4 303–333	Age 5 334–354	Age 6 355–370	Total
ATF≥40cm-w	0	0	4811	0	2406	0	0	7217
ATF≥40cm-sbs	0	0	9419	0	0	0	0	9419
KF≥40cm-sbs	0	0	999	0	0	0	0	999
KF≥40cm-w	0	0	356	0	178	0	0	534
PH≥80cm-c	0	0	8121	8121	0	0	0	16,242
PH5079cm-c	0	1130	2260	0	0	0	0	3390
PH≥80cm-w	0	0	3428	1714	0	0	1714	6856
COD30–59cm-c	0	47,081	0	0	0	0	0	47,081
COD30–59cm-w	0	0	3668	0	0	0	0	3668
COD≥60cm-w	0	7536	22,607	37,679	7536	0	0	75,358
COD≥60cm-c	11,325	28,312	50,962	22,650	0	0	0	113,249
Total	11,325	84,059	106,631	70,164	10,120	0	1714	284,013

Atka mackerel as predator

Atka mackerel have been documented as predators of both planktonic invertebrates and teleosts in both the western and central North Pacific Ocean. Simenstad et al. (1977) found that planktonic crustaceans, hyperiid amphipods, calanoid copepods, and oikopleura (larvaceans) occurred frequently in Atka

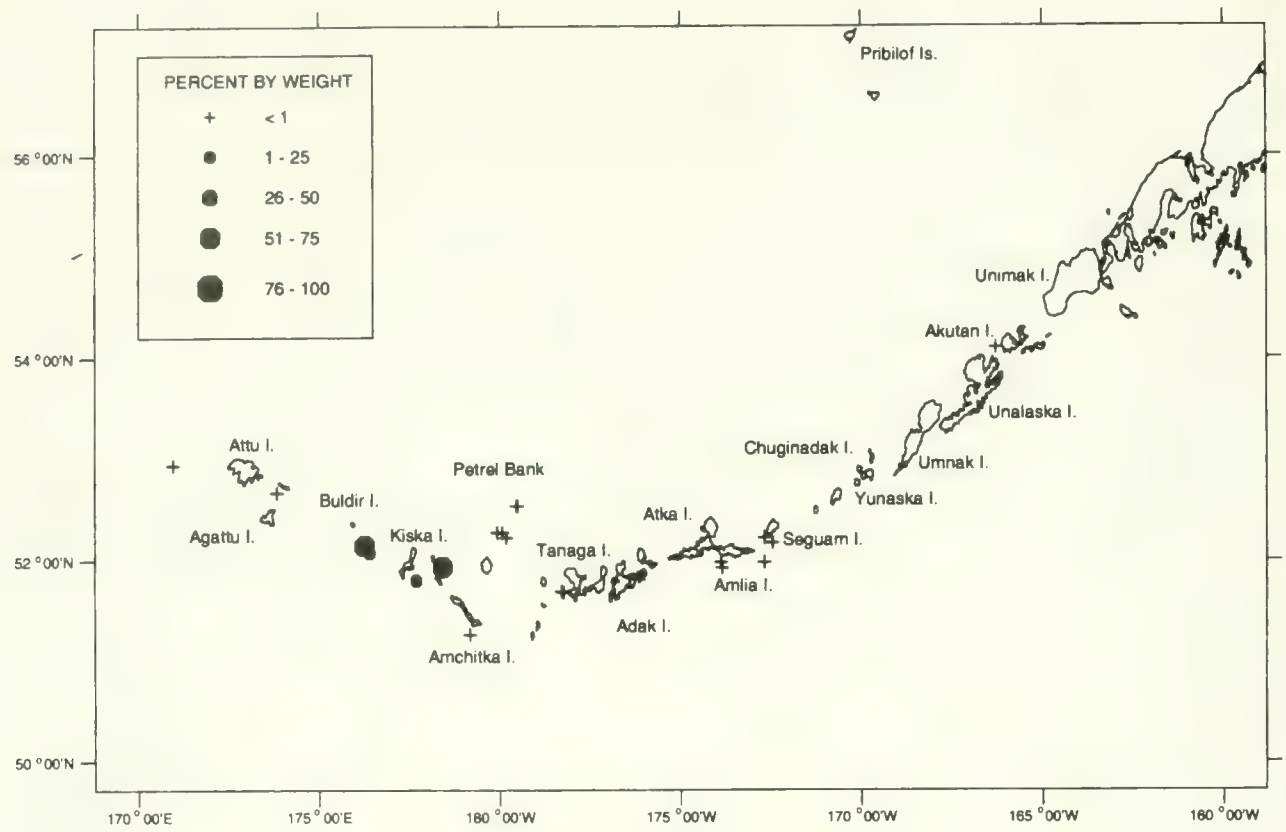

Figure 3

Geographic distribution of eggs cannibalized by Atka mackerel in the Aleutian Islands area in summer 1991.

mackerel stomachs collected from the Amchitka Island area. By contrast, in this study, euphausiids were the most important food (28% by weight). Onishchik (1997) found that myctophids (57% by weight) were the most important food of Atka mackerel in the Kuril Range area even though calanoid copepods and euphausiids occurred more frequently in stomachs. Orlov's study (1997) also showed that Atka mackerel is mainly a planktivore. He found that in the Kuril Islands area, copepods were present in 51% of Atka mackerel stomachs.

Several studies (Takemura and Yamane, 1953; Zolotov and Medveditsyna, 1979; Zolotov and Tokranov, 1991) have shown that Atka mackerel eat their own eggs. I also found evidence of egg cannibalism at four locations near Kiska Island (Fig. 3). I compared the frequency of occurrence of Atka mackerel eggs found at these locations. In three out of four hauls, females cannibalized more eggs than did males. In four hauls, males (n=7–9) exhibited 13–43% frequency of occurrence, and females (n=6–8) exhibited 17–57% frequency of occurrence of egg cannibalism. This finding suggests that male egg-guarding behavior, a characteristic of the species (Zolotov and Tokranov, 1991), may have inhibited the males from feeding on their own eggs. Combining stomach-content data from these four hauls (Table 8) showed that males consumed more euphausiids (27%) and less calanoids (18%), whereas females consumed more calanoids (35%) and less euphausiids (6%) when egg cannibalism occurred. I analyzed the rest of the data (where no egg cannibalism occurred) and found that males and females fed on very similar percentage by weights of calanoids (mainly (*Neocalanus plumchrus*)), euphausiids (mainly *Thysanoessa* spp), and larvaceans (Table 9). On the basis of these data, I hypothesize that egg-guarding behavior may cause some variations in diet of male and female Atka mackerel. All cannibalism occurred in September at depths between 80 and 170 m, indicating that the Kiska Island area may be a spawning ground for Atka mackerel in September. Zolotov and Tokranov (1991) found that, during the spawning season (from August to September), Atka mackerel eggs were the main food of rock mackerel (*Hexagrammos lagocephalus*), Atka mackerel, yellow Irish lord (*Hemilepidotus jordani*), and the common Irish lord (*H. gilberti*).

Table 8

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the main prey groups of Atka mackerel (*Pleurogrammus monopterygius*) where egg cannibalism occurred in the Aleutian Islands area in 1991.

	Male		Female		Total	
Prey name	%W	%FO	%W	%FO	%W	%FO
Gastropoda (snail)	2.66	42.46	1.50	40.77	1.59	41.67
Teuthoidea (squid)	2.05	34.13	1.52	38.69	1.11	36.67
Calanoida (copepod)	18.54	66.02	34.89	77.83	21.30	71.67
Candacia columbiae (copepod)	0.98	49.06	0.80	52.23	0.74	51.67
Gammaridea (amphipod)	4.40	42.11	2.97	37.05	3.79	40.00
Themisto sp. (amphipod)	2.34	63.34	2.93	74.40	1.89	68.33
Euphausiacea (euphausiid)	27.23	49.16	6.14	42.26	19.42	46.47
Caridea (shrimp)	0.05	2.78	0.27	14.43	0.12	8.33
Majidae (spider crab)	0.48	8.68	0	0	0.20	5.00
Chaetognatha (arrow worm)	0.86	12.95	0.05	3.57	0.25	8.33
Larvacea Copelata	11.07	89.73	9.25	89.14	8.76	90.00
Gnathostomata	0.01	3.57	0	0	0.01	1.67
Zoarcidae (eelpout)	5.24	2.78	0	0	3.51	1.67
Pleurogrammus monopterygius (Atka mackerel eggs)	16.66	28.77	32.79	41.67	28.96	35.00
Fishery discards	3.92	3.57	0	0	3.05	1.67
Total prey weight	52 g		25 g		78 g	
Total nonempty stomachs	32		28		60	
Total empty stomachs	0		0		0	
Total hauls	4		4		4	

Table 9

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the main prey groups of the Atka mackerel (*Pleurogrammus monoptgerygius*) that had no egg cannibalism in the Aleutian Islands area in 1991.

	Male		Female		Total	
Prey name	%W	%FO	%W	%FO	%W	%FO
Gastropoda (snail)	0.82	46.77	0.74	30.66	0.71	33.26
Teuthoidea (squid)	0.87	21.75	6.14	30.69	5.51	25.05
Calanoida (copepod)	30.02	60.81	22.08	60.20	23.01	58.63
Candacia columbiae (copepod)	0.32	41.52	0.53	48.36	0.46	43.43
Gammaridea (amphipod)	0.28	15.24	0.08	8.78	0.15	10.80
Themisto sp. (amphipod)	1.95	67.69	3.16	59.03	2.54	57.00
Euphausiacea (euphausiid)	26.78	63.40	31.81	68.63	30.86	63.24
Caridea (shrimp)	0.15	21.95	0.09	15.89	0.10	17.12
Majidae (spider crab)	0.03	4.04	0.05	4.37	0.03	3.53
Chaetognatha (arrow worm)	0.74	29.45	1.28	30.23	1.03	27.33
Larvacea Copelata	14.81	80.65	7.42	66.15	9.12	68.11
Gnathostomata	0.01	0.89	0.03	2.42	0.01	1.66
Myctophidae (lanternfish)	1.18	1.79	0.43	0.84	0.92	1.18
Theragra chalcogramma	2.79	2.81	4.12	2.86	2.96	2.55
Total prey weight	288 g		335 g		623 g	
Total nonempty stomachs	82		89		171	
Total empty stomachs	5		2		7	
Total hauls	14		17		17	

Atka mackerel as prey of marine mammals

Many marine mammals feed on Atka mackerel. Merrick (1995) found that Atka mackerel was the most common prey identified in Steller sea lion scats from the Aleutian Islands from 1990 to 1993. Nemoto (1957) found that Atka mackerel was the preferred food of humpback whales (*Megaptera novaeangliae*) in the waters west of the Attu Islands and the waters south of Amchitka Island. Kasamatsu and Tanaka (1992) stated that in the southwestern Hokkaido region, *Pleurogrammus azonus*, a congener distributed mainly in the northern part of the Sea of Japan, represented 80–100% of the diet of minke whale (*Balaenoptera acutorostrata*). Kenyon (1965) found that 85% (by volume) of the food of harbor seals (*Phoca vitulina*) in the Amchitka Islands area was Atka mackerel. Atka mackerel have also been found in the stomachs of sperm whales (*Physeter macrocephalus*) (Kawakami, 1980), killer whales (*Orcinus orca*) (Nishiwaki and Handa, 1958), fin whales (*Balaenoptera physalus*) (Nemoto, 1957), Dall's porpoise (*Phocoenoides dalli*) (Crawford, 1981; Perez and McAlister, 1993), minke whale (Perez and McAlister, 1993), harbor seal (Perez, 1990), northern fur seals (*Callorinus ursinus*) (Perez, 1990), and sea otters (*Enhydra lutris*) (Kenyon, 1969). Consumption of Atka mackerel at the population level by marine mammals was not estimated in this study because of insufficient data on their biomass, daily ration, and diet of marine mammals.

Atka mackerel as prey of seabirds

Seabirds are important predators in the Aleutian Islands marine ecosystem. Some seabirds feed on fish larvae or young juveniles, and some feed on zooplankton. Ogi (1980) analyzed the prey of 320 thick-billed murres (*Uria lomvia*) that drowned in Pacific salmon gill nets in the oceanic waters ranging from the Kuril Islands to a region east and south of the Aleutian Islands (160°W) and found that juvenile Atka mackerel and several species of lantern fish (Myctophidae) were important prey (17% of the total weight). Wehle (1983) found that Atka mackerel represented 42.3%, by occurrence, of the food of horned puffin (*Fratercula corniculata*), and it occurred in 6.3% of the stomachs of tufted puffin (*F. cirrhata*) at Buldir Island. Hatch and Sanger (1992) found only two Atka mackerel (138 and 139 mm) consumed by the tufted puffin, but Byrd et al.[3] found that Atka mackerel were important food of tufted puffin in 1990 at Buldir Island and Aiktak Island. Consumption of Atka mackerel at the population level by seabirds (like marine mammals) was not estimated in this study because of the lack of quantitative data on the biomass, daily ration, and diet of many seabirds in this area.

[3] Byrd, G. V., J. C. Williams, and R. Walder. 1992. Status and biology of the tufted puffin in the Aleutian Islands, Alaska, after a ban on salmon driftnets. U.S. Fish and Wildlife Service. Alaska Maritime National Wildlife Refuge. Aleutian Islands Unit, PSC 486, Box 5251, FPO AP 96506-5251, Adak, Alaska.

Summary

This study assessed the importance of Atka mackerel in the Aleutian Islands marine ecosystem. As a predator (mainly adults in this study), Atka mackerel were basically zooplanktivores. Calanoid copepods, euphausiids, planktonic tunicates, amphipods, and other crustaceans were principal food items. Atka mackerel also consumed some benthic fishes (cottids and young-of-the-year walleye pollock) and mesopelagic fishes (myctophids and bathylagids) and cannibalized its own eggs. As prey, about 48,500 t of Atka mackerel (mainly age 2+) were consumed by marine fishes. Table 7 indicates that about 26% of the consumed Atka mackerel were age-3 and older. Because of insufficient data, consumption of Atka mackerel at the population level by marine mammals and seabirds could not be estimated. Human beings also consumed a large amount of Atka mackerel. The total commercial catch of Atka mackerel was 26,740 t in 1991 (about 2.2% of the exploitable biomass [age 3+] in that year).

This study provides information about predator-prey relationships between Atka mackerel and their predators (marine fishes, marine mammals, and seabirds), and between Atka mackerel and their prey (zooplankton and other invertebrates) in the Aleutian Islands marine ecosystem. More information about the early life history (eggs, larvae, and juveniles) of Atka mackerel is needed to improve our understanding of their trophic role in the marine ecosystem.

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Ultrasonic telemetry: its application to coral reef fisheries research

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The importance to fisheries research of understanding movement patterns of fishes is increasingly being recognized (Hilborn and Walters, 1992). Traditionally, mark-recapture studies with external tags constituted the major method of examining movements in fishes (Shepherd, 1988). However, external tagging techniques are known to have several limitations (reviewed by Kearney, 1989) that often cannot be addressed adequately. In particular, data obtained through conventional tagging studies are usually limited to knowledge of a single point of capture, point of recapture, and the straight line distance and time interval between these two events. Such data can be misleading because the exact distance traveled and the patterns of movement are unknown. However, such patterns are of major importance to current research efforts in tropical reef fisheries, including investigations of spawning aggregation events (Samoilys and Squire, 1994; Zeller, 1998), and to the assessment of movements in relation to marine reserves (e.g. Russ and Alcala, 1996).

Ultrasonic telemetry is an ideal tool to address questions of movement and activity patterns of fishes. It can be used effectively under circumstances that limit the use of more traditional methods, yet its suitability for fisheries research is only slowly being realized (Nelson, 1990). Reviews of telemetry in the aquatic environment are provided by Harden-Jones and Arnold (1982), Hawkins and Urquhart (1983) and Nelson (1990).

Ultrasonic telemetry has been little used on coral reef fishes (e.g. Holland et al., 1993; Tulevech and Recksiek, 1994); most studies have concentrated on sharks (Nelson, 1990). Recent studies, however, have successfully applied the present techniques to the serranid *Plectropomus leopardus* (Zeller, 1997, 1998; Zeller and Russ, 1998), the primary target species of line fisheries on the Great Barrier Reef, Australia (Kailola et al., 1993).

The aims of this study were the assessment of ultrasonic telemetry in the coral reef environment and the application of the technique to *P. leopardus*. The first objective was the determination of a suitable transmitter placement technique and anesthetic. The second objective consisted of a field evaluation of ultrasonic telemetry. The final objective comprised tracking trials of *P. leopardus*.

Materials and methods

Study location and ultrasonic telemetry equipment

The study was conducted during 1993 at Lizard Island Research Station, northern Great Barrier Reef, Australia (lat. 14°40'S; long. 145° 28'E). The telemetry equipment consisted of V8-2L transmitters and a VR60 receiver linked to a directional 50–80 kHz hydrophone (Vemco Ltd, Halifax, Canada).

Evaluation of fish anesthetics and transmitter placement techniques

Fish (size range: 34.0 cm–52.5 cm fork length [FL]) were caught on hand lines. Aquarium facilities included 500-, 1000-, and 2000-L tanks with continuous flow-through water supply. Stocking densities did not exceed 2 fish/500 liters. Specimens were retained for an acclimation period (1–3 days), and were not fed for 24 hours prior to the experiments.

The first concern was that of procuring a successful, deep anesthesia that allowed a gentle recovery in the fish. Three anesthetics were tested: 1) Hypnodil™ (Janssen Pharmaceutica, active ingredient: metomidate) was used at a concentration of 7 mg/L (Mattson and Riple, 1989); 2) phenoxyethanol was used at a concentration of 0.5 ml/L (Mattson and Riple, 1989); and 3) MS-222 (tricaine methanesulfonate) was used at a concentration of 80 mg/L (Thomas and Robertson, 1991).

Three methods were used to attach telemetry units to the animals: 1) stomach placement (force feeding) by means of oral insertion of the transmitter into the stomach (e.g. Holland et al., 1992)—the least intrusive method, neither resulting in external protrusion of the unit, nor requiring surgery; 2) external placement by attaching transmitters directly to the dorsal musculature (Holland et al., 1996); and 3) internal placement by inserting transmitters into the body cavity as described by Hart and Summerfelt (1975) and Holland et al. (1993). Surgical implements were disinfected in ethanol and soaked in Tamodine™, a fish-antiseptic solution (Vetark Professional, Winches-

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ter, UK). The incision was placed parallel to the midventral line on the left hand side of the fish, 2 cm anterior to the anus and 1–2 cm lateral of the midventral line. Three to four rows of scales were removed from the area of planned incision, and the area was cleaned with Tamodine™. A 2–3 cm anterior-posterior incision was made into the body cavity. Disinfected transmitters were coated in antiseptic cream prior to careful insertion into the body cavity. The incision was closed with 6–8 surgical staples (Ethicon Proximate III™) as suggested by Mortensen (1990), the area was cleaned with Tamodine™, and the fish given an intraperitoneal injection of antibiotic (tetracycline 50 mg/kg of fish, McFarlane and Beamish, 1990), before being returned to the aquarium tanks.

Aquarium experiments Owing to limited aquarium space, it was not possible to evaluate all combinations of anesthetics and placement methods simultaneously. Hence two separate experiments were conducted. Experiment A examined the least intrusive transmitter placement technique (force feeding) with all three anesthetics. In experiment B the two intrusive techniques (external attachment and insertion into the body cavity) were tested in conjunction with the two most suitable anesthetics.

Experiment A: force feeding All three anesthetics were tested with force feeding to assess differences in retention times of transmitters due to the anesthetic agent. It was hypothesized that use of the hypnotic agent Hypnodil™ (metomidate) would result in the longest retention times owing to the low stress levels caused by this compound (Thomas and Robertson, 1991). *Plectropomus leopardus* regurgitate stomach contents easily, particularly when exposed to stressful conditions.[1]

Twenty-one specimens of *P. leopardus* (size range: 39.0 cm–52.5 cm FL) were assigned randomly to the three anesthetic treatments (n=7). Individual fish were anesthetized, tagged with T-bar anchor tags for identification, their fork length was measured, individually numbered transmitters were inserted into the stomach, and fish returned to the aquaria for recovery. Fish were fed daily. Aquaria were examined for regurgitated transmitters every two hours during daytime and once during the night. The start of each inspection was taken as the maximum retention period for any recovered units.

[1] Davies, C. 1992. Cooperative Research Centre for Reef Research, James Cook University of North Queensland, Townsville, 4811, Australia. Personal commun.

Experiment B: external attachment and surgical insertion The suppression of a stress response due to the use of metomidate (Hypnodil™) makes this a valuable drug for the routine handling of fishes (Thomas and Robertson, 1991). However, slightly elevated levels of the stress hormone corticosteroid are considered beneficial for resistance to trauma, thus making metomidate less suitable in situations involving stress, such as surgical procedures (Thomas and Robertson, 1991). Given the nature of the intrusive manipulations performed in experiment B, the use of Hypnodil™ was discontinued.

Experiment B compared two anesthetic agents (phenoxyethanol and MS-222) and two transmitter placement methods (external attachment and surgical insertion) in a full factorial design. The transmitter placement factor consisted of five treatment levels: external and internal placement treatments, external and internal placement controls, and a routine handling control. All fish received the same preliminary handling: fish were anesthetized, weighed (to the nearest 50 g), measured (fork length), and tagged externally. Routine-handling control fish were returned to the aquaria. The external attachment treatment consisted of attaching transmitters *sensu* Holland et al. (1996), and injecting an antibiotic intraperitoneally (tetracycline 50 mg/kg of fish, McFarlane and Beamish, 1990), before fish were returned to the aquarium. The procedure lasted 5–8 minutes. External-attachment control fish underwent the same procedure, but a transmitter was not attached after puncturing the musculature, and the fish were returned to the aquaria after eight minutes. The internal placement treatment consisted of surgical insertion of the transmitters into the body cavity as described above. The procedure took 15–20 minutes. Internal placement control fish were treated identically, but no transmitter was placed in the body cavity prior to closure of incisions. Fish were returned to the aquaria after 20 minutes.

Twenty *P. leopardus* were used (size range: 34.0–50.7 cm FL), resulting in two random replicates per treatment combination. Fish were fed daily, and each individual was examined visually without handling, to record general condition, behavior, feeding and wound status. The experiment was terminated after 24 days because gas-bubble-trauma (Weitkamp and Katz, 1980) affected the behavior (lethargy and cessation of feeding) of fish from all experimental groups. Upon termination, wounds were examined and classified as aggravated (ripped, or inflamed [secondary infection]), partially healed (40–50% wound closure), or healed (possibly minor inflammation). Subsequently, transmitters were removed and fish were weighed.

Data analysis Data from experiment A were analyzed for differences in retention times between anesthetic agents by using a single-factor analysis of covariance (ANCOVA). Fork length was used as a covariate to account for any effect of size of fish on the retention times. Assessment of experiment B was based on the observations made during and after the experiment. The change in weight during experiment B was analyzed by using a two-factor analysis of covariance (ANCOVA). Occurrence of gas-bubble-trauma was treated as a covariate. Underlying assumptions were evaluated prior to analyses (Sokal and Rohlf, 1981).

Field evaluation of ultrasonic telemetry in the coral reef environment

The extensive use of radio telemetry in wildlife research has produced procedures to assess the accuracy (bias and precision) of telemetry reception (White and Garrott, 1990). However, no such procedures appear to be published for ultrasonic telemetry. Given the paucity of studies with ultrasonic telemetry in the coral reef environment, a standardized field test using stationary transmitters was undertaken. Given that wind and sea-state influence the detectability of sound transmission in water (Jellyman et al., 1996), any effect of direction of prevailing wind on detectability or directional bias of observed sound signals needed to be assessed. Thus, the objectives of this field evaluation were 1) to establish the accuracy of directional bearings in relation to prevailing wind direction; 2) to evaluate observer bias and precision of bearings in relation to wind direction; and 3) to determine the optimal angle for cross-bearings, and the optimal distance between tracking boat and signal in order to obtain position estimates that minimize error polygons.

Experimental methods An ultrasonic transmitter (V8-2L, Vemco Ltd) was attached 15 cm above the substratum to a surface buoy in 4–6 m water depth. Three 200-m transects were run from the moored transmitter in relation to the prevailing wind direction:

0°: transmitter located directly upwind from any position on the transect.
45°: transmitter located at 45° downwind from the prevailing wind direction.
90°: transmitter located at right angle to the prevailing wind direction.

Marker buoys were positioned at 25-m intervals along each transect, starting at 50 m from the transmitter location (i.e. from 50 to 200 m), resulting in 21 positions for the three transects. Replicated compass bearings to the transmitter were obtained for each position by using the following protocol: the field of view of the observer was restricted to the tracking receiver for the duration of the experiment; an assistant anchored the boat at the marker buoys in random order and recorded the true compass bearing to the transmitter. The observer determined the perceived maximum directional signal strength by using the directional hydrophone. The corresponding compass bearing of the directional hydrophone (observed bearing) was recorded. The direction of the hydrophone was changed haphazardly by the assistant and the procedure was repeated. Six replicate bearings were taken at each of the seven distances on the three transects. The procedure was repeated by the second observer for a total of 252 observed bearings.

Data analysis Data were assessed for accuracy, bias, and precision (White and Garrott, 1990). Bearing error polygons were determined by using the largest and smallest directional bearing observed at each distance-marker buoy for any combination of two transects (0°–45°, 45°–90°, and 0°–90°). Thus, the error polygon parameters obtained (polygon area and maximum diagonal dimension) represented the largest possible error polygon estimates. Only bearing pairs from equidistant locations were used for polygon determination. Statistical analyses included Kruskal-Wallis nonparametric ANOVA and paired *t*-test. All data were examined for violations of underlying assumptions prior to analysis (Sokal and Rohlf, 1981) and data $\log_{10}$ transformed where applicable. Given that the angular scale of measurement represented only part of a circle, and absolute direction of angles was of no interest, data were treated as linear (Cain, 1989).

Field tracking trials

To verify the findings from the aquarium study, the two most suitable long-term transmitter placement techniques (external and internal placement) were tested under field conditions (MS-222 used as anesthetic). Two *P. leopardus* (43.1 cm and 58.9 cm FL) were equipped with external transmitters and released at their capture site after a 15-min recovery period. In the second field trial, internal transmitters were placed in two specimens (59.0 cm and 42.9 cm FL). Fish were released at the capture site after recovery from anesthesia.

The basic tracking technique described by Holland et al. (1985, 1992) was used. Exact positions of fish equipped with transmitters were determined by visual

triangulation (White and Garrot, 1990) by using identifiable landmarks and reef features. Triangulation involves the estimation of the location of a transmitter by using two or more directional bearings obtained from a known location (White and Garrot, 1990). Visual triangulation uses visible land and reef features that can be identified from maps or aerial photographs, in conjunction with directional bearings to identify the location of the transmitter.

Results

Evaluation of fish anesthetics and transmitter placement techniques

Experiment A: force feeding Gastric retention times of force-fed transmitters ranged from 18 to 216 hours; longer retention periods were documented for larger fish (Fig. 1, r=0.621, n=21). Mean retention times differed between anesthetic agents used (ANCOVA, $F_{2,17}$=4.762, P=0.023). The use of MS-222 resulted in a shorter retention time compared with either phenoxyethanol (SNK, P=0.004) or metomidate (SNK, P=0.001). Mean retention times did not differ with the use of either phenoxyethanol or metomidate (SNK, P=0.216). On average, fish anesthetized with MS-222 retained the transmitters for 42.0 hours (±9.7 SE), in contrast with fish anesthetized with phenoxyethanol (118.0 hours [±17.2 SE]) and metomidate (147.4 hours [±23.8 SE]).

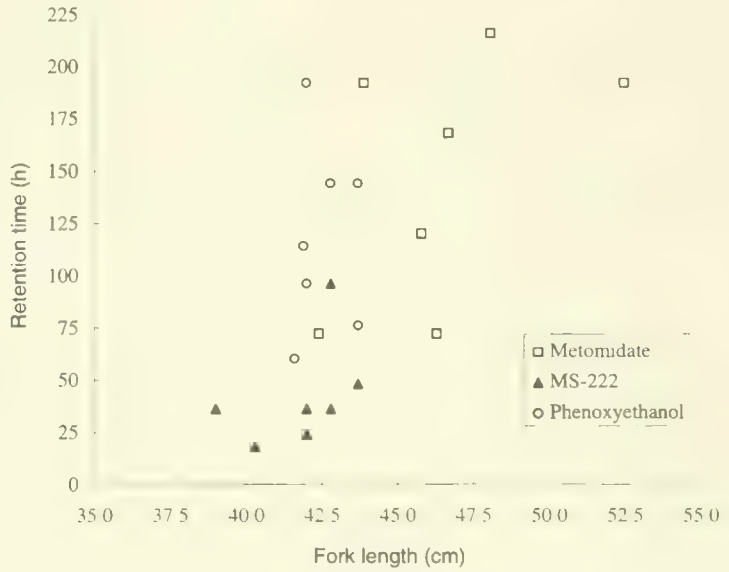

Figure 1

Correlation of gastric retention time of force-fed transmitters versus fork length of *P. leopardus*, as determined in experiment A (n=21, r=0.62). The three anesthetic agents are indicated.

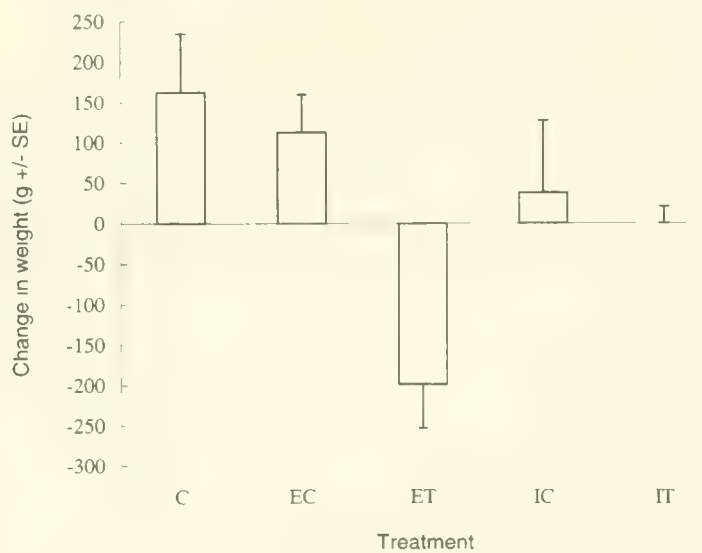

Figure 2

Change in mean weight (before treatment to after treatment) of *P. leopardus* as determined in experiment B. Note: negative weight indicates a loss in weight and vice versa. Presented are means (g ±SE). Treatments: C = routine handling control; EC = external attachment control; ET = external attachment treatment; IC = internal placement control; IT = internal placement treatment. n = 20.

Experiment B: external attachment and surgical insertion The change in weight of fish over the duration of the experiment differed significantly between transmitter placement treatments (ANCOVA, $F_{4,9}$= 5.309, P=0.018). Fish carrying external transmitters displayed a substantial reduction in weight compared with fish in all control groups that gained weight, whereas the internal treatment group showed no change in mean weight during the experiment (Fig. 2). Fish with external transmitters were observed spending a lot of time rubbing the attached transmitter against the substratum. Furthermore, most fish started feeding within two days, except for fish in the external treatment group and those anesthetized with phenoxyethanol in the internal control group (Table 1).

Table 1

Observations for aquarium experiment B. Treatment: C = routine handling control; EC = external attachment control; ET = external attachment treatment; IC = internal placement control; IT = internal placement treatment. Anesthetic: MS = MS-222; P = phenoxyethanol. "—" indicates that specimen never resumed feeding after treatment.

Treatment	Type of anesthetic	Level of anesthesia achieved	Day of first feeding	Affected by gas-bubble-trauma	Wound status
C	MS	deep	2	Y	—
C	MS	deep	2	N	—
C	P	twitching	2	N	—
C	P	deep	2	N	—
EC	MS	deep	—	Y	partially healed
EC	MS	deep	2	N	healed
EC	P	deep	—	Y	partially healed
EC	P	twitching	2	Y	healed
ET	MS	deep	10	Y	aggravated
ET	MS	deep	—	Y	aggravated
ET	P	deep	10	N	aggravated
ET	P	twitching	7	N	aggravated
IC	MS	deep	2	N	healed
IC	MS	deep	2	N	healed
IC	P	deep	7	Y	healed
IC	P	deep	7	N	healed
IT	MS	deep	2	N	healed
IT	MS	deep	2	N	healed
IT	P	deep	2	N	healed
IT	P	twitching	—	Y	healed

Observational records illustrated some differences in the effects of the anesthetics. All fish anesthetized with MS-222 attained deep anesthesia, whereas 40% of fish exposed to phenoxyethanol did not (Table 1). This resulted in twitching of the animal during treatment. Occasional cramp-like convulsions were also observed in some of these specimens during the early recovery period.

Examination of placement wounds after the termination of the experiment revealed consistent patterns (Table 1). The incisions made into the body cavities of internal control and internal treatment fish were healed (some minor inflammations did exist). The puncture wounds through the dorsal musculature of fish with externally attached transmitters were aggravated and in some cases enlarged due to repeated attempts to dislodge the transmitters. Wounds on external control fish were either healed or partially healed, and there were no further signs of aggravation.

Field evaluation of ultrasonic telemetry in the coral reef environment

Evaluation of bearing errors (true bearing-observed bearing) by transect (0°, 45° vs. 90°) indicated a significant difference in mean bearing error between transects (Kruskal-Wallis $H_{2,252}$=22.102, P= 0.000). The 90° transect displayed the least bias (mean=–1.50° ±0.7163° SE), the 0° transect had slightly larger, positive bias (mean=2.09° ±1.077°SE), and the 45° transect showed strong, negative bias (mean=–5.43° ±1.021°SE).

Owing to the differences in bias and accuracy between transects, observer differences in bias were examined separately for each transect. Bias differed between observers for the 0° transect (Kruskal-Wallis $H_{1,84}$=6.238, P=0.013); observer two showed positive bias compared with observer one (Fig. 3). Observers did not differ significantly in bias for the 45° transect (Kruskal-Wallis $H_{1,84}$=0.209, P=0.648, Fig. 3), or the 90° transect, (Kruskal-Wallis $H_{1,84}$=2.603, P=0.107, Fig. 3).

Paired t-tests were used to compare precision estimates (SD) between observers for each transect separately. No significant observer difference in precision was detected: 0° (t_6=1.2599, P=0.2545), 45° (t_6=1.5819, P=0.1648) and 90° (t_6=0.6859, P=0.5184).

Evaluation of the parameters of maximum-error polygons indicated some clear patterns, both with respect to distance between sound source and tracking boat and with respect to angular combination of position bearings taken. The 0°–45° transect combina-

tion generally produced the largest error polygon area and length estimates, regardless of distance between sound source and tracking boat (Fig. 4). The 45°–90° transect combination produced similar results, with the exception of 50 m distance, where this combination resulted in the smallest polygon area and length (Fig. 4). Overall, however, the 0°–90° transect combination consistently resulted in the smallest polygon parameter estimates, irrespective of distance from which bearings were taken (Fig. 4). The best results for this angle combination were obtained at distances of 50 to 75 m from the sound source, with maximum-error polygon diameters of 58.5 m and 34.5 m, respectively.

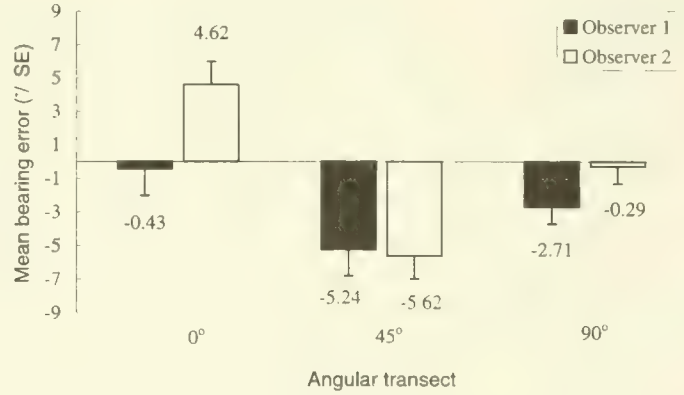

Figure 3

Mean bearing errors (±SE, n=42) for each observer on each angular transect, illustrating the difference in observed bias between the two observers for the transect facing directly into the prevailing wind (i.e. 0°). Mean values are indicated.

Field tracking trials

The two fish tagged with external transmitters did not travel far. The larger specimen traveled less than 25 m, whereas the smaller fish moved a maximum of 60 m. Both fish spent considerable time inside the shelter of the reef matrix, with the result that a low acoustic signal was received, accompanied by reduced reception angles. This behavior was confirmed during visual observations. The tracking trial was terminated after four days, and both fish were collected. Both specimens exhibited aggravated external wounds. Repeated dislodgment attempts, or snagging of the external transmitter on reef substratum had resulted in enlarged external wounds and loosened transmitters.

The two fish with surgically implanted transmitters took shelter inside the reef matrix immediately after release (observed on snorkel) and were not resighted. The signal weakened once the specimens had taken shelter, and remained weak for 48 hours. By the third day both signals were received strong and clear in the same location. Visual confirmation indicated that both transmitters were inside a whitetip reef shark (*Triaenodon obesus*). The immediate, postsurgery release of *P. leopardus* had resulted in mortality due to predation within 48–72 hours after release.

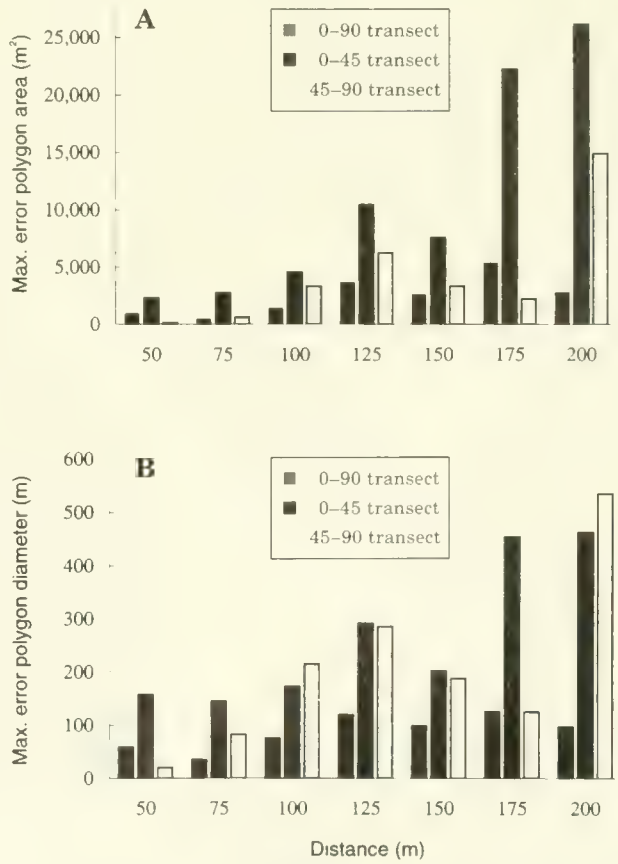

Figure 4

Maximum-error polygon parameters for each identical distance pair for the three possible angular transect combinations. Error polygons were calculated by using the largest and smallest angular bearings recorded from equidistant positions for each of the three possible angle combinations during the evaluation trials. Data pooled for observers. (**A**) Maximum error polygon area (m²). (**B**) Maximum diameter of error polygon (m).

Conclusions and recommendations

Transmitter placement and fish anesthetics

The aquarium experiments illustrated that, although surgical insertion is technically the most difficult method, it provided the least side effects

and should be selected for longer term studies, especially for bottom-associated reef fishes. Wound closure was observed within 14–21 days, and subsequent research (Zeller, 1997, 1998) illustrated that secondary infections were reduced with the use of a broad-spectrum bacteriacide (Myxazin™, Waterlife Research Industries, Longford, UK) and oral antibiotic (tertracycline). After the initial occurrence of gas-bubble-trauma (Weitkamp and Katz, 1980), the aquarium water was filtered through gravel prior to use. No further incidents of gas-bubble-trauma occurred (Zeller, 1997, 1998).

Releasing the experimental tracking specimens immediately after intrusive surgery meant releasing an injured fish that became a prime target for reef fish predators. All subsequent tracking specimens were retained for a recovery period in aquaria until the implant incision was healed (2–3 weeks). This procedure proved to be successful during subsequent studies and no further fatalities due to predation were observed (Zeller, 1997, 1998).

This study demonstrated clearly that external attachment of transmitters is not a viable option for *P. leopardus* because fish are disturbed by the external package and attempt to dislodge the devices. However, a study on a reef-associated carangid, a species with a more pelagic lifestyle, reported successful use of external transmitters (Holland et al., 1996). This finding illustrates the necessity of evaluating transmitter placement techniques in relation to species and species-specific habits.

Force feeding was demonstrated to be of use with *P. leopardus* only for short-term duration not exceeding a few days. Even the longest retention time recorded (216 hours) was considered unsatisfactory for longer term tracking studies (Zeller, 1997, 1998).

Tricaine methanesulfonate (MS-222) was the best anesthetic because it induced a successful loss of sensation and a gentle recovery, with the potential additional benefit of improved recovery from physical trauma because it elevated levels of the corticosteroid hormone (Thomas and Robertson, 1991). Furthermore, unlike with phenoxyethanol, Losey and Hugie (1994) did not observe any negative effects with MS-222 in regard to the olfactory sense. The present findings suggest that MS-222 represents the most suitable anesthetic for the surgical placement of transmitters.

Ultrasonic tracking of coral reef fishes

The following considerations will improve position estimation for tracking studies on coral reefs, and have been applied successfully (Zeller, 1997, 1998; Zeller and Russ, 1998): manual tracking with visual triangulation should be conducted by taking bearings at approximately right angles (90°) to each other and with approximate distances of 50–75 m between vessel and transmitter. Bearings taken at angles less than 90°, or taken at sharp angles to the prevailing wind, should be avoided. These considerations will result in minimal directional bias of bearings and ensure maximum accuracy and precision of estimates. If uncertainty about location or directionality of signal exists, it is suggested that "ground-zero tracking" (Nelson, 1990) be used to verify exact location of tracking specimen.

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Announcement

The editorial staff of *Fishery Bulletin* would like to thank the following referees for their time and efforts in providing reviews of the manuscripts published in 1998–1999. Their contributions have helped ensure the publication of quality science.

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